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A REVISION OF *PHILODENDRON* SUBGENUS *PHILODENDRON* (ARACEAE) FOR MEXICO AND CENTRAL AMERICA[1]

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Abstract

This is the first revision of *Philodendron* subg. *Philodendron* since that of K. Krause in *Das Pflanzenreich* in 1913. *Philodendron* subg. *Philodendron*, the largest of the three subgenera, includes 103 taxa (95 species and 8 subspecies or varieties) for Central America. Sixty-eight taxa are new to science. These include 62 species: *P. albisuccus* Croat, *P. alticola* Croat & Grayum, *P. angustilobum* Croat & Grayum, *P. annulatum* Croat & Grayum, *P. antonioanum* Croat, *P. aromaticum* Croat & Grayum, *P. bakeri* Croat & Grayum, *P. breedlovei* Croat, *P. brewsterense* Croat, *P. brunneicaule* Croat & Grayum, *P. chiriquense* Croat, *P. chirripoense* Croat & Grayum, *P. clewellii* Croat, *P. coloradense* Croat, *P. copense* Croat, *P. correae* Croat, *P. cotobrusense* Croat & Grayum, *P. cotonense* Croat & Grayum, *P. crassispathum* Croat & Grayum, *P. cretosum* Croat & Grayum, *P. dodsonii* Croat & Grayum, *P. dolichophyllum* Croat, *P. dominicalense* Croat & Grayum, *P. dwyeri* Croat, *P. edenudatum* Croat, *P. ferrugineum* Croat, *P. findens* Croat & Grayum, *P. folsomii* Croat, *P. fortunense* Croat, *P. gigas* Croat, *P. granulare* Croat, *P. grayumii* Croat, *P. hammelii* Croat, *P. hebetatum* Croat, *P. heleniae* Croat, *P. immixtum* Croat, *P. jefense* Croat, *P. knappiae* Croat, *P. lazorii* Croat, *P. lentii* Croat & Grayum, *P. llanense* Croat, *P. madronense* Croat, *P. malesevichiae* Croat, *P. morii* Croat, *P. niqueanum* Croat, *P. pirrense* Croat, *P. pseudauriculatum* Croat, *P. purulhense* Croat, *P. roseospathum* Croat, *P. scalarinerve* Croat & Grayum, *P. sousae* Croat, *P. squamicaule* Croat & Grayum, *P. squamipetiolatum* Croat, *P. straminicaule* Croat, *P. sulcicaule* Croat & Grayum, *P. thalassicum* Croat & Grayum, *P. tysonii* Croat, *P. ubigantupense* Croat, *P. utleyanum* Croat, *P. verapazense* Croat, *P. wilburii* Croat & Grayum, *P. zhuanum*; 6 infraspecific taxa: *P. davidsonii* Croat subsp. *bocatoranum* Croat, *P. hederaceum* (Jacq.) Schott var. *kirkbridei* Croat, *P. ligulatum* Schott var. *heraclioanum* Croat, *P. ligulatum* Schott var. *ovatum* Croat, *P. roseospathum* Croat var. *angustilaminatum* Croat, *P. wilburii* var. *longipedunculatum* Croat & Grayum; and 2 new combinations: *P. hederaceum* (Jacq.) Schott var. *oxycardium* (Schott) Croat, *P. radiatum* Schott var. *pseudoradiatum* (Matuda) Croat. Species diversity of *P.* subg. *Philodendron* in Central America shows a general diminution from Mexico to Middle America, followed by a marked increase closer to South America. Mexico has 21 taxa, Guatemala 15, Belize 9, El Salvador 5, Honduras 13, Nicaragua 18, Costa Rica 49, and Panama 80, respectively. Endemism is high, especially for Panama where 39 taxa are currently considered endemic. Mexico and Costa Rica each have 7 endemic species. With the exception of Belize, which has 1 endemic, no other country in Middle America has any endemic species. Only 26 species (28 taxa), a total of 26% of all Central American species, range into South America, 8 species (7% of the total) only to Colombia.

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Introduction

Philodendron is, after *Anthurium*, the largest genus in the Araceae, with 700 or more species (Croat, 1979, 1983a, 1988, 1990). This is the first major revision of *P.* subg. *Philodendron* for Central America since Kurt Krause's (1913) generic treatment in *Das Pflanzenreich. Philodendron* is one of the most important genera in the Neotropics, inhabiting a wide range of mesic habitats from sea level to over 2000 m and in life zones (Holdridge, 1967) ranging from *Tropical moist forest* to *Premontane rain forest.* While most species occur in virgin humid forests, the genus is known from freshwater swamps, stream banks, regrowth forest, rock outcrops, and roadbanks. It is not only one of the largest genera in the Neotropics but also often constitutes the most conspicuous element of the vegetation because of its abundance, primarily climbing habit, and frequently large, showy leaves. The genus provides a wide variety of choice ornamental plants for horticulture, including most of the species treated here. Unfortunately, it is also still poorly known taxonomically, especially in the South American Andes.

Philodendron has 119 Central American species comprising 128 taxa, distributed in two subgenera of *Philodendron.* This Central America revision encompasses only members of *P.* subg. *Philodendron,* with 103 taxa, including 95 species and 8 varieties or subspecies (Appendix 1, Geographic Distribution of Central American *Philodendron* subg. *Philodendron*). A total of 68 taxa are new to science: 62 species, 6 subspecies or varieties, and 2 combinations. Alternatively, *P.* subg. *Pteromischum,* revised separately by Grayum (1996), contains 21 species (26 taxa) for Central America. That revision encompasses all species from Pacific and Caribbean tropical America, ignoring only species from the region of the Guianas and from the Amazon drainage of South America.

Philodendron is a distinct genus, not easily confused with any other, though closest to *Homalomena,* which differs in having a consistently terrestrial habit, frequently spiny petioles, a sap smelling of anise, and staminodia among the pistillate flowers.

Species diversity of *P.* subg. *Philodendron* in Central America shows a general diminution from Mexico to Middle America with the lowest totals just north of the San Juan depression, followed by a marked increase approaching the South American continent. Mexico has 21 taxa, Guatemala 15, Belize 9, El Salvador 5, Honduras 13, Nicaragua 18, Costa Rica 48, and Panama 82. Endemism is high, especially for Panama where 39 taxa are currently considered endemic. Mexico and Costa Rica each have 7 endemic species. With the exception of Belize, which has 1 endemic, no other country in Middle America has any endemic species.

Most of the Central American species of *P.* subg. *Philodendron* (Appendix 3, Sectional Composition of *Philodendron* subg. *Philodendron* in Central America) are in *P.* sect. *Calostigma* (Schott) Engl. with 52 taxa (48 species) and *P.* sect. *Philodendron* with 62 taxa (58 species). Other sections represented in Central America are: *P.* sect. *Tritomophyllum* (Schott) Engl. with 6 species; *P.* sect. *Polytomium* (Schott) Engl. with 3 species (4 taxa); and *P.* sect. *Macrogynium* Engl. with 1 species. Sections not represented in Central America are: *Schizophyllum* (Schott) Engl.; *Camptogynium* K. Krause; and *Philopsammos* G. S. Bunting. A key for the sections of *P.* subg. *Philodendron* is included under "Taxonomy."

Materials and Methods

This revision is based on more than 25 years of field studies in Central and South America, between 1967 and 1993. All but 15 of the 95 species were studied in the field or under cultivation at the Missouri Botanical Garden. Those only known from herbarium material are: *P. breedlovei, P. brewsterense, P. chirripoense* Croat & Grayum, *P. cotobrusense, P. dwyeri, P. folsomii, P. hammelii, P. jefense, P. madronense, P. roseospathum* var. *angustilaminatum, P. sousae, P. ubigantupense, P. utleyanum,* and *P. verapazense* Croat. Except for these, all descriptions have been prepared from both living and dried specimens. The use of ("dried") preceding all or any part of the description is an indication that all that follows is based on herbarium material only. Morphological characters were coded directly into a computerized database to ensure parallel and sortable descriptions. The aroid descriptions database, completely rewritten since the publication of my revision of *Anthurium* sect. *Pachyneurium* (Croat, 1991), contains 892 character states used to describe the morphological diversity expressed in *Philodendron.* A total of 108 of these are used exclusively for description of the bisexual inflorescence (and thus were not used in the descriptions of *Philodendron*), while 220 describe unisexual inflorescences. The database also allows for sorting of characters for use in writing keys or in providing useful lists of characters for preparing a cladistic survey. In addition, the database can be put to future use for the preparation of floristic surveys or for adding additional newly discovered species. The description database is tied directly to the nomen-

clatural database in TROPICOS (Crosby, 1986; Crosby & Magill, 1986). Finally, discussions and references to illustrations as well as exsiccatae are stored separately but tied to a particular species description and to the nomenclatural information by a unique taxon number. Specimens can be added to the exsiccatae almost until the time of publication because they are automatically presorted to localities before being printed. Species descriptions are decoded into narrative text automatically before final editing for style.

Terminology and usage in the descriptions in this revision are largely defined by Croat and Bunting (1979). Further definitions of petiole cross-sectional shapes are defined and illustrated in Croat (1983a). The colors reported in the description frequently are taken from the color chart by Berlin and Kay (1969) and are referenced in the text as B & K. This color chart, available from the University of California Press, is a reproduction of the Munsell Color Array of 40 hues, at maximum saturation, with nine degrees of brightness. This represents 40 hues in the vertical columns and 9 degrees of brightness in the horizontal columns. Colors are arranged in 10 basic clusters with 4 different hues per cluster, ranging from red through yellow, green, blue, purple, and finally red-purple. The four columns for each color cluster are numbered 2.5, 5, 7.5, and 10. These numbers are repeated for each basic color type. The colors from the B & K color chart are read by first reporting the color, then the row followed by the column. For example, the third color in the fifth row is Red 5/7.5. The second color in the eighth row is Red 8/5.

Ecological zones, though sometimes estimated from my own experience with Central American vegetation, are largely taken from Holdridge life-zone maps (Holdridge, 1967; Holdridge et al., 1971), where they exist for Central American countries. Vegetation types for Mexico are taken from the "Mapa de tipos de vegetación de la República de Mexico" (Flores et al., 1971).

Each life zone is represented by a full textual statement and abbreviation which appear on life zone maps. The Holdridge Life Zones of Central America and areas where *Philodendron* occur are listed here, arranged in a generally drier to wetter order: *Tropical thorn woodland* (T-tw); *Tropical dry forest* (T-df); *Tropical moist forest* (T-mf); *Tropical wet forest* (T-wf); *Tropical rain forest* (T-rf); *Premontane thorn woodland* (P-tw); *Premontane moist forest* (P-mf); *Premontane wet forest* (P-wf); *Premontane rain forest* (P-rf); *Tropical Lower Montane wet forest*; (TLM-wf); *Tropical Lower Montane rain forest* (TLM-rf); *Tropical wet forest* transition to *Premontane wet forest* (T-wf/P-wf); *Premontane wet forest* transition to *moist forest* (P-wf/mf); and *Premontane wet forest* transition to *rain forest* (P-wf/rf).

Herbarium material has been widely distributed, and original field vouchers are cited for all herbaria whose material was seen. Herbarium material may consist of one of three kinds: (1) complete original sets (wild collected); (2) sterile original material with an inflorescence added from a cultivated plant of the same number; and (3) material collected entirely from cultivated plants. Specimens based entirely or in part on cultivated material are clearly indicated on the herbarium label.

Herbarium specimens were borrowed from most major herbaria including: AAU, B, BBS, BISH, BM, BR, CAS, CAY, CM, COL, CR, DAV, DUKE, DS, EAP, ECON, ENCB, F, FLAS, FSU, FTG, G, GH, HBG, ISC, K, L, LA, LL, LE, M, MEXU, MICH, NY, PMA, RSA, S, SCZ, SEL, TEX, U, UC, UMO, US, VEN, and WIS.

Descriptions are mostly parallel and as complete as possible. Descriptions of the pistils, vitally important in the infrageneric classification of *Philodendron*, are particularly detailed. In order to avoid repetition, description references are made to Style Types discussed by Mayo (1986). These style types are discussed and illustrated (Fig. 469) in the introduction under the section on "Morphology of Reproductive Structures—Gynoecium."

Infraspecific categories in this work adhere to the following definitions. Subspecies are those infraspecific taxa that are mostly or entirely allopatric either geographically, elevationally, or ecologically. Varieties, though morphologically distinct in one or several characters, are apparently geographically, elevationally, or ecologically sympatric. All infraspecific taxa within Central American *Philodendron* subg. *Philodendron* are ecologically sympatric.

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This revision could not have been completed without the help of many people, most important among them my dedicated and able co-worker, Petra Malesevich, who participated in nearly every phase of the work. I could count on her to continue the research unabated during my long field trips. Along with Bob Magill, she revised, updated, and improved the more powerful description program that we used for the *Philodendron* revision. Jo Ann Beiser played an important role for nearly two years, providing assistance in the preparation of descriptions. Kathy Pickett Upton, former Research Greenhouse manager, played a major role in maintaining the live collections, making pollinations,

and in dealing with label problems. Very special thanks also go to my colleague and fellow aroid specialist Mike Grayum, whose knowledge of the Costa Rican Araceae is without parallel. He has not only made many of the best collections of *Philodendron*, but his breadth of experience in that part of Central America and his vivid insights into the interrelationships of species were very rewarding. In addition, his skills as an editor and his knowledge of Latin and rules of nomenclature contributed much to this work. Simon Mayo, like Mike Grayum, conducted extensive work on *Philodendron*. Their work was concurrent or preceded my own, and their ideas and interpretations of phenomena in the genus were ever insightful. My own work has benefited greatly from their work. Dan Nicolson was always generous with his time in helping to solve nomenclatural problems as well as problems with translations of difficult Latin phraseology. Gordon McPherson provided pickled material of many species of *Philodendron* during his tenure as our resident botanist in Panama. Eleanor Sauer has proofread or written Latin diagnoses for nearly all of the new species. Joseph Tosi, of the Tropical Science Center in San José, Costa Rica, assisted us in standardizing our use of the Holdridge Lifezone System, which we have added to our computerized database. Leland Russell, summer volunteer and later summer employee while vacationing from his undergraduate studies at Carleton College in Minnesota, became very skillful at dissections of *Philodendron* inflorescences. His critical comparative study of the Central American species of *Philodendron* went a long way in increasing our understanding of the differences within the genus. Finally, I would like to thank my wife, Patricia, who has without complaint allowed me to spend several months each year wandering the tropics of Central and South America for almost three decades. She was always available to solve every computer glitch and has also helped with the computerized sorts of information which led to the construction of the keys.

History of the Genus *Philodendron*

Although *Philodendron* apparently figured in pre-Columbian folklore, art, and medicine during the 16th century, and herbarium material was collected by Georg Marcgraf as early as 1644 (Mayo, 1990), it was Charles Plumier who made the first effective introduction of the genus to European scientists (Mayo, 1990). He collected five or six species from Martinique, St. Thomas, and Hispaniola, giving phrase names beginning with "Arum" or "Dracunculus." See Mayo (1990) for a detailed account of *Philodendron* collections made by other late 17th-century and 18th-century explorers, including Hans Sloane in Jamaica and N. J. Jacquin in the West Indies, Colombia, and Venezuela.

Plumier's expeditions resulted in the first species of *Philodendron* to be published as new to science, albeit as an *Arum*, *A. lingulatum* L., a member of *Philodendron* subg. *Pteromischum*. His trips also resulted in *Philodendron hederaceum*, the first member of *P.* subg. *Philodendron* to be published new to science, as *Arum hederaceum* Jacq.

Heinrich Wilhelm Schott

One hundred thirty-six years passed from the time Plumier first introduced plants of what came to be known as *Philodendron* to European scientists in 1693 and the first circumscription of the genus by Schott in 1829. During this interim a number of workers, including Carl Linnaeus, worked with generic concepts and decided that not all aroids belonged in the same genus. *Arum* came to be used only for the European plants it now represents and *Arisaema*, *Dracunculus*, and *Colocasia* were also separated by the early 18th century (Hermann, 1698; Tournefort, 1700). By the fifth edition of *Genera Plantarum* Linnaeus (1754) had recognized also *Calla*, *Dracontium*, and *Pothos* as well as *Orontium*, *Pistia*, and *Acorus*, although not recognizing the last three as related to *Arum*.

By the middle of the 18th century the exploration of the Neotropics was well under way. The introduction of so many new plants from the New World tropics, including many *Philodendron* species, made it clear that further separation was needed. Because of the uncritical acceptance of many aberrant elements into *Arum* during the course of the 18th century a number of taxa now recognized as *Caladium*, *Philodendron*, and *Syngonium* were incorporated into *Arum*. Ventenant (1800) solved part of the problem by recognizing *Caladium*, but Willdenow (1805) erred in transferring into *Caladium* four of Jacquin's West Indian *Philodendron* species (all considered *Arum* at the time).

Even by the time of the 16th edition of *Systema Vegetabilum* Sprengel (1826) did not distinguish *Philodendron* but had increased the number of genera to 12, adding *Ambrosina*, *Arisarum*, *Caladium*, *Gymnostachys*, and *Zantedeschia*.

Resolution of many of the remaining generic problems with the Araceae awaited Austrian botanist Heinrich Wilhelm Schott, who was the first to focus on the taxonomy of the Araceae (Nicolson, 1960). Schott was uniquely qualified in this regard, having spent four years in Brazil collecting plants

and with access to the large collection of living plants at the Imperial Gardens [of the Hapsburg's] at Schönbrunn Palace in Vienna where he worked as the director. These included his own Brazilian collections as well as those of N. J. Jacquin from the Caribbean. In 1829 Schott described the genus *Philodendron* (published as *Philodendrum*) Schott in one of his first publications after returning from Brazil in 1821. The first species placed in the genus were: *P. grandifolium* (Jacq.) Schott, *P. laciniosum* Schott, *P. tripartitum* (Jacq.) Schott, *P. lacerum* (Jacq.) Schott, *P. pinnatifidum* (Jacq.) Schott, and *P. hederaceum* (Jacq.) Schott. In 1832 Schott published a preliminary classification of the Araceae in a work entitled *Meletemata Botanica*, which included many plant families and was done in conjunction with his colleague S. Endlicher. In this work he recognized 39 genera of Araceae including *Philodendron* and some other by now well known species-rich genera such as *Anthurium, Syngonium, Dieffenbachia, Aglaonema,* and *Spathiphyllum.* In this work he also published the first infrageneric system of classification for *Philodendron*, although it contained only three groups still recognized today. Though Schott subsequently continued to work on his circumscription of the genera and species of the Araceae for the remainder of his career, he did not publish any major revisions of Araceae for 24 years.

Endlicher (1837), publishing alone but with the obvious assistance of Schott (Mayo, 1990), produced a revision of *Philodendron* that differed from the *Meletemata Botanica* account by Schott only in having a more complete generic description, including vegetative details which were presented for the first time.

Shortly after Endlicher's revision, K. S. Kunth (1841) published in his "Enumeratio Plantarum. . ." the first species-level revision of *Philodendron.* This revision included new species and new combinations and for the first time included species of the genus that would later be recognized as members of *P.* subg. *Pteromischum.*

It was not until Schott's (1856) publication of a work entitled *Synopsis Aroidearum* that a fully developed infrageneric system of classification was realized. This was Schott's first species-level revision of the genus, and the *Synopsis* divided the genus into 22 "greges" grouped in 7 unnamed categories arranged in increasing order of complexity of leaf blade shape (Mayo, 1990). A total of 99 species (which was recognized here for the first time as grex *Pteromischum*) and 3 species of *P.* subg. *Meconostigma* were included (two of them reported as members of grex *Sphincterostigma*).

Schott's final classification of *Philodendron* was published four years later in the *Prodromus Systematis Aroidearum* (1860), a more rigorous work that came to be his last comprehensive self-published work, since he died at the age of 71 in 1865. This revision included 110 genera; almost all are still recognized as genera or subgenera. The fact that his work has stood the test of time is a testimony to the serious nature of the research he had done in Vienna during his long period of seeming inactivity.

Schott's treatment of *Philodendron* in the *Prodromus* differed from his revision in the *Synopsis* in having more complete descriptions, using more inflorescence characters; in having six rather than seven unnamed categories of leaf shape to group the "greges"; and in beginning to make use of the cataphyll (prophyll in the strictest modern sense) as a character. Schott used the term "subopposite stipule" for the feature that came to be known as the cataphyll in Engler's usage. This has proven to be one of the best and most reliable characters for the genus. For a detailed listing of the key characters for *Philodendron* used in Schott's *Prodromus* revision, refer to Mayo (1990: 50).

The *Prodromus* treatment included 135 species of *Philodendron* included in the same "greges." Twenty species of the total were members of *P.* subg. *Pteromischum* Schott and 6 species are now placed in *P.* subg. *Meconostigma* (Schott) Engl. (3 in grex *Meconostigma* and 3 in grex *Sphincterostigma*). Thus Schott included 110 names of *P.* sect. *Philodendron.* Taking synonymy into account, only 76 species of *P.* sect. *Philodendron* were included in this 1860 revision. Only 18 names pertained to Central America. Of these, only 8 are accepted members of *P.* sect. *Pteromischum.*

The species included by Schott (1860) in each grex of the *Prodromus* for Central America are listed below:

Grex *Baursia* Rchb. ex Schott: *P. wendlandii* Schott
Grex *Pteromischum* Schott: *P. aurantiifolium* Schott, *P. ligulatum* (L.) K. Koch, *P. seguine* Schott, *P. inaequilaterum* Liebm.
Grex *Canniphyllum* Schott: (no species represented)
Grex *Glossophyllum* Schott: (no species represented)
Grex *Solenosterigma* Klotzsch: *P. oxycardium* Schott, *P. micans* K. Koch, *P. scandens* K. Koch & Sello = (*P. hederaceum*)
Grex *Psoropodium* Schott: *P. tenue* K. Koch & Augustin, *P. gracile* Schott

Grex *Achyropodium* Schott: *P. verrucosum* L. Mathieu ex Schott
Grex *Platypodium* Schott: *P. pterotum* K. Koch & Augustin, *P. fragrantissimum* (Hook.) Kunth
Grex *Cardiophylacium* Schott: *P. brevispathum* Schott, *P. hederaceum* Schott (= *P. jacquinii* Schott)
Grex *Belocardium* Schott: *P. hoffmannii* Schott, *P. advena* Schott, *P. acrocardium* Schott
Grex *Cardiobellium* Schott: (no species represented)
Grex *Meconostigma* Schott: (no species represented)
Grex *Eubelium* Schott: (no species represented)
Grex *Macrolonchium* Schott: (no species represented)
Grex *Macrobelium* Schott: *P. daemonum* Liebm. = *P. sagittifolium* Liebm., *P. sagittifolium* Schott, *P. tanyphyllum* Schott = *P. sagittifolium* Liebm.
Grex *Imbéa*: (no species represented)
Grex *Oligophlebium* Poepp.: (no species represented)
Grex *Doratophyllum* Schott: (no species represented)
Grex *Schizophyllum* Schott: (no species represented)
Grex *Tritomophyllum* Schott: *P. tripartitum* (Jacq.) Schott, *P. dagilla* Schott = *P. tripartitum* (Jacq.) Schott, *P. anisotomum* Schott
Grex *Polytomium* Schott: *P. subincisum* Schott, *P. impolitum* Schott = *P. radiatum* Schott, *P. polytomum* Schott = *P. radiatum* Schott, *P. warszewiczii* K. Koch & Bouché
Grex *Sphincterostigma* Schott: (no species represented)

In all, only 18 of the 135 species of *Philodendron* included in this 1860 revision were from Central America, and 4 of the total were members of *P.* grex *Pteromischum.* One of the four species, *P. ligulatum* Schott, is a member of *P.* sect. *Philodendron,* which Schott had inadvertently placed in his grex *Pteromischum.* Five of Schott's names became *P. hederaceum* (*P. acrocardium, P. hoffmannii, P. oxycardium, P. scandens,* and *P. micans),* but the count was reduced by only four since the name *P. hederaceum* was involved in two currently accepted species (namely, *P. hederaceum* and *P. jacquinii*). Other reductions are *P. gracile,* which is a synonym of *P. tenue*; *P. daemonum* and *P. tanyphyllum,* which are synonyms of *P. sagittifolium*; *P. dagilla,* a synonym of *P. tripartitum*; and *P. impolitum* and *P. polytomum,* synonyms of *P. radiatum.* Thus Schott was dealing with only 16 (16.5%) of the 96 currently known Central American species.

ADOLF ENGLER

Little was done with *Philodendron* following Schott's death in 1865 until Adolf Engler, working at the Universities of Kiel and Breslau (and finally at the Berlin Botanical Garden), began his revisionary work on the Araceae. Schott had laid the groundwork, describing most of the genera that still exist today, but he was dealing with only a small portion of the species. Taking up his first positions at Kiel and Breslau in 1871, at age 27, Engler worked with various tropical families on the *Flora Brasiliensis* project, publishing and working on a general review of the vegetative and floral morphology for the entire family (Engler, 1877). Later, in his powerful position as Director of the Berlin Botanical Garden, Engler commanded attention and a wealth of herbarium specimens and living material from all over the world during Germany's preeminent period of domination in the botanical world preceding World War II. Since Engler was only 21 at the time of Schott's death, it is not likely that the two ever met, but Engler would have had access to some of the same material, including living material from the Schönbrunn greenhouses, as well as Schott's notes and illustrations made over a 40-year period (Engler, 1876). Unlike modern workers, he had access to Schott's herbarium in Vienna before it was destroyed during World War II. This is important for a continuum of species concepts in groups often described from inadequate material of unknown origin and worse yet sometimes destroyed by war.

Engler's (1878) treatment of the Araceae in Martius's *Flora Brasiliensis* included 116 species of *Philodendron,* 95 of which were members of *P.* sect. *Philodendron* (13 were in *P.* sect. *Pteromischum* and 8 in *P.* sect. *Meconostigma* (Schott) Engl.). Only 47 species of *Philodendron* were then known from Brazil. The work also included sectional and species descriptions as well as a key to all existing species of *Philodendron.* In this work Engler modified Schott's system of classification for *Philodendron* by recasting Schott's "greges" as sections and reducing the number from 22 to 10. He also synonymized a number of species, reducing the total from 132 to 116 species. Only a single Central American species, *P. oxycardium* (= *P. hederaceum* var. *oxycardium*) was reported for Brazil, a fairly accurate picture as we know today. Only a couple of other species, namely *P. fragrantissimum* and *P. verrucosum,* have been found to range into the Am-

azon drainage of South America. Two additional species, *P. glanduliferum* Matuda and *P. brevispathum*, have a subspecies or variety that occurs in the Amazon basin of South America, but the same do not occur in Central America.

In the following year Engler's treatment of *Philodendron* for A. and C. DeCandolle's *Monographie Phanerogamarum* (Engler, 1879) was essentially unchanged, adding only 3 species to bring the total to 120. Of these, 93 species were members of *P.* subg. *Philodendron* and 20 of the epithets represented species currently known from Central America (now reduced to 15 through synonymy).

The final revisionary effort by Engler on *Philodendron* published 20 years later (Engler, 1899) was changed only slightly at the subgeneric level from the 1878 work. One section was raised to subgeneric status, and the remaining nine sections were included in *P.* subg. *Euphilodendron* Engl. (now *P.* subg. *Philodendron*). Despite minor changes made by Krause (1913), it is essentially Engler's classification that persists almost a century later. Engler's (1899) revision was substantially larger than Schott's last revision. Engler's revision contained 167 species, 134 of them in *P.* subg. *Philodendron*, with 23 reported for Central America (reduced to 15 species through synonymy in this revision). One species, *P. purpureoviride* Engl., reported for Ecuador, is now known for Central America.

The species of *P.* subg. "*Euphilodendron*" included in Engler's (1899) revision broken down by section for Central America are listed below:

P. sect. *Pteromischum* Schott: *P. aurantiifolium* Schott (as synonym of *P. guttiferum* Kunth), *P. guatemalense* Engl., *P. inaequilaterum*, *P. seguine*, *P. talamancae* Engl.
P. sect. *Baursia* (Rchb. ex Schott) Engl.: *P. wendlandii* Schott
P. sect. *Polyspermium* Engl.
"Gruppe" *Platypodium* Schott: *P. pterotum*
"Gruppe" *Solenosterigma* Klotzsch: *P. oxycardium* (= *P. hederaceum* var. *oxycardium*), *P. purpureoviride* (as *P. purpureoviridis* from South America), *P. micans* K. Koch (= *P. hederaceum* var. *hederaceum* forma *micans*), *P. scandens* (= *P. hederaceum* var. *hederaceum*)
"Gruppe" *Cardiobelium* Schott: *P. brevispathum*, *P. gracile* (= *P. tenue*), *P. schottianum*, *P. tenue*
"Gruppe" *Achyropodium* Schott: *P. verrucosum*
P. sect. *Oligospermium* Engl.
"Gruppe" *Macrobelium* Schott: *P. sagittifolium*, *P. daemonum*, *P. sanguineum* Regel (= *P. sagittifolium*), *P. mexicanum* Engl.
"Gruppe" *Belocardium* Schott: *P. ligulatum* Schott, *P. advena*, *P. subovatum* Schott (= *P. advena*), *P. smithii* Engl.
"Gruppe" *Oligocarpidium* Engl.: *P. pittieri* Engl. (= *P. hederaceum*)
P. sect. *Tritomophyllum* (Schott) Engl.: *P. anisotomum*, *P. tripartitum*, *P. fenzlii* Engl. (= *P. tripartitum*)
P. sect. *Schizophyllum* (Schott) Engl.: no species represented
P. sect. *Polytomium* (Schott) Engl.: *P. augustinum* K. Koch (= *P. radiatum*), *P. radiatum* Schott, *P. warszewiczii* K. Koch & Bouché
P. sect. *Macrolonchium* (Schott) Engl.: *P. fragrantissimum*
P. sect. *Macrogynium* Engl.: *P. hoffmannii* Schott sensu Engl. (= *P. jacquinii* Schott)

The turn of the century saw major activity with *Philodendron*, no doubt due to Engler's just published revision. Engler made no changes in his revision but went on to publish 26 additional species (Engler, 1905b). In addition, seven species were described by Alfred Barton Rendle, Ignaz Urban, Ambroise Gentil, and N. E. Brown between 1901 and 1908.

KURT KRAUSE

Kurt Krause, who began working with Engler at the Berlin Botanical Garden on 1 January 1905, described two additional species before preparing his revision of *Philodendron* for *Das Pflanzenreich* (Krause, 1913). The latter remains the most recent revision of the whole genus. Krause's revision is a slightly reworked version of Engler's (1899) revision but did include the description of a new section, *P.* sect. *Camptogynium*, with a single species in *P.* subg. *Philodendron* ("*Euphilodendron*") and included 55 more species. There were 32 other new species published in *P.* subg. *Philodendron*. Six of these were in *P.* sect. *Pteromischum* (*P.* subg. *Pteromischum*), while one was in *P.* subg. *Meconostigma*. The remaining 25 were in *P.* subg. *Philodendron*. Most were members of *P.* sect. *Baursia* and *P.* sect. *Polyspermium* (*Philodendron*) with a single species each in the following sections: *Oligospermium* (*Calostigma*), *Schizoplacium*, *Macrolonchium*; and three species in *P.* sect. *Polytomium*. Only two species, *P. grandipes* K. Krause and *P. panamense* K. Krause (both in current *P.* sect. *Philodendron*), were from Central America. Krause's treatment of *P.* subg. *Philodendron* included the following sections and species for Central America (or at least now known from Central America):

Names used by Krause (1913) and their current status. Species numbers refer to those in Krause's revision.

2. *P.* sect. *Baursia* (Rchb. ex Schott) Engl.
   39. *P. wendlandii* Schott
3. *P.* sect. *Polyspermium* Engl.
   67. *P. coerulescens* Engl. (member of *P.* subg. *Pteromischum* mistakenly placed here)
   70. *P. pterotum* K. Koch & Augustin
   77. *P. grandipes* K. Krause
   90. *P. purpureoviride* Engl. (reported for Ecuador)
   95. *P. scandens* K. Koch & Sello = *P. hederaceum*
   96. *P. oxycardium* Schott = *P. hederaceum* var. *oxycardium*
   99. *P. micans* K. Koch = *P. hederaceum* var. *hederaceum* forma *micans*
   108. *P. schottianum* H. Wendl. ex Schott
   110. *P. panamense* K. Krause
   117. *P. gracile* Schott = *P. tenue* K. Koch & Augustin
   116. *P. tenue* K. Koch & Augustin
   125. *P. verrucosum* L. Mathieu ex Schott
4. *P.* sect. *Oligospermium* Engl.
   134. *P. sagittifolium* Liebm.
   140. *P. sanguineum* Regel = *P. sagittifolium* Liebm.
   147. *P. mexicanum* Engl.
   150. *P. ligulatum* Schott
   164. *P. subovatum* Schott = *P. sagittifolium* Liebm.
   168. *P. smithii* Engl.
   173. *P. advena* Schott
   176. *P. pittieri* Engl. = *P. hederaceum* (Jacq.) Schott
5. *P.* sect. *Tritomophyllum* (Schott) Engl.:
   181. *P. fenzlii* Engl. = *P. tripartitum* (Jacq.) Schott
   182. *P. anisotomum* Schott
   183. *P. tripartitum* (Jacq.) Schott
6. *P.* sect. *Schizophyllum* (Schott) Engl.: (no species represented in Central America).[3]
7. *P.* sect. *Polytomium* (Schott) Engl.:
   195. *P. radiatum* Schott
   198. *P. augustinum* K. Koch = *P. radiatum* Schott
   199. *P. polytomum* Schott = *P. radiatum* Schott
   200. *P. warszewiczii* K. Koch & Bouché
8. *P.* sect. *Macrolonchium* (Schott) Engl.
   202. *P. fragrantissimum* (Hook.) Kunth
9. *P.* sect. *Macrogynium* Engl.
   207. *P. hoffmannii* Schott sensu Engl. = *P. jacquinii* Schott
10. *P.* sect. *Campogynium* K. Krause: (no species represented in Mesoamerica)

The 28 Central American species names for *Philodendron* subg. *Philodendron* represented only 11% of the 222 species in Krause's revision. Of the 28 taxa Krause reported for Central America, *P. coerulescens* was a member of *P.* subg. *Pteromischum*, 10 are now considered synonyms of other Central American species which he also reported or which have been subsumed into other species as varieties or subspecies. Of the ten, two, *P. tenue* and *P. jacquinii*, have been given older names that he did not report but still represent Central American species. Thus, Krause's revision of *Philodendron* of Central America treated only 19 species, roughly ⅓ of the total currently known for Central America. One additional Central American species, *P. purpureoviride*, was treated by Krause but not reported for Central America.

MODERN WORK

Since no revisionary work took place on *Philodendron* between the time of Krause and the advent of *Philodendron* specialist George Bunting's (1963a) revisionary work, most species were described as the result of floristic work and most of these were from South America. In all, 142 new species epithets for *Philodendron* have been introduced to date since the time of Krause's revision (including 5 species published by Grayum, 1992b). In addition, 11 new varieties, 7 new subspecies, and 1 new form were published during this period. Six new combinations were made. Of this total only 33 species of *Philodendron* were reported for Central America, and 11 of these were in *P.* subg. *Pteromischum*. Thus 22 species of *P.* subg. *Philodendron* were published between the last full revision of the genus by Krause and the completion of the current work (not including those species of *P.* subg. *Pteromischum* in Grayum (1996)). The Mesoamerican taxa of *P.* subg. *Philodendron* described between the time of Krause's revision and the completion of this work are as follows: *Philodendron apocarpum* Matuda (= *P. jacquinii* Schott), *P. auriculatum* Standl. & L. O. Williams, *P. basii* Matuda, *P. brenesii* Standl., *P. davidsonii* Croat, *P. dressleri* G. S. Bunting, *P. erlansonii* I. M. Johnst. (= *P. jacquinii*), *P. glanduliferum* Matuda, *P. harlowii* I. M. Johnst. = *P. hederaceum*, *P. jamapanum* G. S. Bunting (= *P. sagittifolium* Liebm.), *P. jo-*

[3] *Philodendron pedatum* (Hook.) Kunth was reported by John Hall of Costa Rica but no live or dried material is available for confirmation.

davisianum G. S. Bunting, *P. lancigerum* Standl. & L. O. Williams (= *P. sagittifolium*), *P. latisagittium* Matuda (= *P. mexicanum*), *P. lundellii* Bartlett ex Lundell (= *P. jacquinii*), *P. microstictum* Standl. & L. O. Williams, *P. miduhoi* Matuda = *P. hederaceum*, *P. mirificum* Standl. & L. O. Williams (= *P. pterotum* K. Koch & Augustin), *P. monticola* Matuda = *P. advena*, *P. platypetiolatum* Madison, *P. pleistoneurum* Standl. & L. O. Williams (= *P. grandipes* K. Krause), *P. pseudoradiatum* Matuda (= *P. radiatum* var. *pseudoradiatum* (Matuda) Croat), and *P. trisectum* Standl. (= *P. anisotomum*).

Three additional species were described in *Philodendron* but actually pertain to other genera (see under "Excluded Names").

Many of the other taxa in Krause's revision were synonymized or reduced in rank, and only 11 taxa in *P.* subg. *Philodendron* remained. These were: *P. brenesii*, *P. radiatum* var. *pseudoradiatum*, *P. auriculatum*, *P. microstictum*, *P. basii*, *P. glanduliferum*, *P. dressleri*, *P. jodavisianum*, *P. platypetiolatum*, *P. davidsonii*, and *P. strictum*.

Most of the Central American floristic work outside of Mexico was carried out by Paul C. Standley, often working with his associate Louis O. Williams. Standley worked initially at the Smithsonian and later at the Field Museum in Chicago, then at the herbarium of the Escuela Agrícola Panamericana, where he died at Zamorano in Honduras. Standley described *P. brenesii* and *P. trisectum* (= *P. anisotomum* Schott) alone, and with L. O. Williams he also provided the following epithets: *P. armigerum* (= *Syngonium armigerum* (Standl. & L. O. Williams) Croat), *P. auriculatum*, *P. brevinodum* (= *Monstera tuberculata* Lundell var. *brevinoda* (Standl. & L. O. Williams) Madison), *P. hastiferum* (= *Syngonium hastiferum*), *P. lancigerum* (= *P. sagittifolium*), *P. microstictum*, *P. mirificum* (= *P. pterotum*), and *P. pleistoneurum* (= *P. sagittifolium*). It is unusual that despite the fact that there were many undescribed species of *Philodendron* subg. *Philodendron* in Costa Rica and Panama, these workers did not succeed in describing many of them since of the nine described, three proved to belong to other genera, and three others proved to be synonyms of existing *Philodendron* names. This is particularly surprising since both Standley and L. O. Williams were astute observers who were very familiar with the Central American flora in general. Their mistakes point out the complexity of the taxonomy of Araceae and the bewildering array of material available to them at that time. Even when I began my own work with the Araceae in the late 1960s there were few specimens (aside from types) that proved to have the correct names. Specimens were often poorly preserved and inadequate, and virtually all lacked good field notes. Either field observations or well-prepared field notes describing aspects of the plants not available on dried plants are essential to the proper understanding of *Philodendron* and other Araceae. I believe that it is possible that this confusion, coupled with the dearth of well-prepared specimens and the paucity of types of Araceae, discouraged workers from making decisions about which species were new.

Perhaps owing to the difficulty with the genus, local floras in Central America were often inadequately done, even if one considers that fewer specimens were available to the authors than today. The treatment of the *Flora of Panama* (Standley, 1944), for example, is woefully inadequate considering the small percentage of the total aroid flora that is covered compared to what is now known to exist.

In his treatment of some genera Standley (1944) seemed too willing to accept epithets of species described in Colombia, regardless of how well they "fit" Panamanian species. As a result many species names in genera such as *Anthurium*, for example, were wrong. His treatment of *Philodendron* subg. *Philodendron* was much better from the standpoint of correct names, but he treated only 8 of the 104 taxa (7%) of *Philodendron* subg. *Philodendron* now known for Panama. Only one species, *P. hoffmannii* (now *P. jacquinii*), had the wrong name. *Philodendron jacquinii* was also misapplied, being intended by Standley for *P. hederaceum*. The other species he included in the *Flora of Panama* were: *P. brenesii*, *P. brevispathum*, *P. grandipes*, *P. panamense*, *P. radiatum*, *P. tripartitum*, and *P. wendlandii*. He did not do so well with members of *P.* subg. *Pteromischum*, where *P. karstenianum* Schott was a mixture of two species and *P. guttiferum* was a mixture of three species. Perhaps the most curious thing about Standley's *Flora of Panama* treatment is that by 1944, after Robert Woodson and his collaborators had already made several expeditions to Panama, so few of the new species included in the present revision had been collected. Standley had collected some of the new species but failed to recognize them as new. These included: *P. crassispathum* (*Standley & Valerio 51910*), *P. findens* (*Standley & Torres 52355*), *P. purulhense* (*Standley 89902*), *P. strictum* (*Standley 51371*), *P. verapazense* (*Standley 91978*), and *P. wilburii* var. *wilburii* (*Standley 38300*). See discussion of those species for additional details. See also section on "Collecting History of *P.* subg. *Philodendron*."

The *Flora of Guatemala* (Standley & Steyermark, 1958b) was much more accurate and complete in the percentage of the total taxa of *P.* subg. *Philo-*

dendron included. However, this probably has less to do with the fact that it was published 14 years later than it does with the fact that there are fewer, generally more widespread species occurring there than in Panama. *The Flora of Guatemala* treated 11 species of *Philodendron*, 8 of them members of *P.* subg. *Philodendron*. These were: *P. anisotomum*, *P. hederaceum*, *P. hoffmannii* (= *P. jacquinii*), *P. radiatum*, *P. sagittifolium*, *P. smithii*, *P. tripartitum*, and *P. warszewiczii*. With 50% of the present total taxa included and with all but one of the taxa still properly bearing the name, the Guatemala treatment remains generally more useful than that of the *Flora of Panama*. Added to the flora since the 1958 revision are: *P. advena*, *P. fragrantissimum*, *P. glanduliferum*, *P. jodavisianum*, *P. mexicanum*, *P. purulhense*, and *P. verapazense*.

The *Flora of Guatemala* (Standley & Steyermark, 1958b) treated *P. hederaceum* correctly but treated *P. jacquinii* under its synonym, *P. hoffmannii*. Curiously, however, the illustration used represents both species. The leaf and stem seem clearly to be *P. hederaceum*, but the inflorescence clearly shows the long-protruded styles of *P. jacquinii*.

Standley's (1937) treatment of the Araceae of Costa Rica was reasonably good, partly because many species had been described by Schott from collections made by H. Wendland in Costa Rica. Other widespread species whose taxonomy had been well established were also a part of the flora. Properly named Costa Rican species recognized by Standley were: *P. brenesii*, *P. ligulatum*, *P. pterotum*, *P. radiatum*, *P. schottianum*, *P. tripartitum*, *P. verrucosum*, and *P. wendlandii*. Species now synonymized are: *P. gracile* (= *P. tenue*), *P. hoffmannii* (= *P. jacquinii*), *P. pittieri* (= *P. hederaceum*), and *P. trisectum* Standl. (= *P. anisotomum*). It has never been determined which species he included under the name *P. panamense*, but that species is not known for Costa Rica. Thus, with 8 out of the 13 names correct and 3 additional species that at least represent synonyms of currently recognized species, Standley did pretty well. However, with only 13 of the current 49 species treated (26%), the treatment was no more complete than that of the *Flora of Panama*, which was written a few years later.

Though no other floristic taxonomist had such a prominent role with Central American *Philodendron* as Standley, there were others who described *Philodendron* during the course of their floristic work.

Ivan M. Johnston of the Arnold Arboretum described *Philodendron erlansonii* (= *P. jacquinii*) and *P. harlowii* (= *P. hederaceum*) while working on the flora of San José Island (Johnston, 1949) of Panama.

In Mexico, Eizi Matuda, the local aroid specialist, described seven species (Matuda, 1954): *P. apocarpum* (= *P. jacquinii*), *P. basii*, *P. glanduliferum*, *P. latisagittium* (= *P. mexicanum*), *P. miduhoi* (= *P. hederaceum*), *P. monticola* (= *P. advena*), and *P. pseudoradiatum* (= *P. radiatum* var. *pseudoradiatum*); and George Bunting described four species during his investigations of Mexican Araceae (Bunting, 1965): *P. dressleri*, *P. jamapanum* (= *P. advena*), *P. jodavisianum*, and *P. tuxtlanum* G. S. Bunting (= *P. sagittifolium*).

Matuda's treatment of the *Philodendron* in Mexico (Matuda, 1954) dealt with 16 species, 13 of them in *P.* subg. *Philodendron*. While a number of the species had the correct names, e.g., *P. advena*, *P. mexicanum*, *P. pseudoradiatum*, *P. radiatum*, and *P. tripartitum*, others had synonymous names, e.g., *P. sanguineum* and *P. daemonum* (both currently recognized as *P. sagittifolium*). Matuda also recognized *P. mexicanum* under three different names, namely *P. mexicanum*, *P. latisagittatum*, and *P. sagittifolium* (a distinct species that he treated as both *P. daemonum* and *P. sanguineum* (a currently recognized name improperly used; see above). Matuda redescribed two species using the names *P. apocarpum* and *P. miduhoi* (currently *P. jacquinii* and *P. hederaceum*, respectively). Finally, he described *P. monticola* (now considered synonymous with *P. advena*).

Other Central American species of *P.* subg. *Philodendron* published since the time of Krause's revision and prior to the beginning of this project in 1986 are *P. davidsonii* and *P. platypetiolatum*, the latter described from Ecuador during Mike Madison's extensive work with the flora of Ecuador during his tenure at the Selby Botanical Garden. Thus, up to the initiation of the current study, only 26 species in *P.* subg. *Philodendron* were described for Central America. With 96 species of *P.* subg. *Philodendron* now known for Central America, this registers an increase of 70 species or a 270% increase.

Of the species of *P.* subg. *Philodendron* described since Krause's revision (not including the present effort) only seven were described by nonspecialists (I. M. Johnston, P. C. Standley, and Standley and L. O. Williams). Standley, together with L. O. Williams, described most of the new Central American species and wrote most of the floristic treatments of the Araceae for Central America. Despite his extensive experience, I do not believe that Standley fully understood the diversity of the Araceae. This is because he failed to recognize a rel-

atively large number of species that were new to science. In Standley's defense it must be stated that the Araceae are a particularly complex family with so much interspecific variation that proper decisions often cannot be easily made without direct comparisons of living material. In addition, collections in the past often had few or no field notes to use for study.

COLLECTING HISTORY

In addition to the history of revisionary efforts it is instructive to consider the collecting efforts in Central America that have laid the groundwork for the scientific work done with *Philodendron* subg. *Philodendron.* Perhaps owing to their sometimes intimidating size, the difficulty of retrieval, and certainly due to the difficulty of preparing and drying specimens, members of *P.* subg. *Philodendron* have never been popular with botanical collectors. The early neotropical collectors, i.e., Ruiz and Pavon, Sessé and Moçiño, Triana and Planchon, and others collected few Araceae (or at least few survived to modern times). Eduard Poeppig, working in Peru, and Richard Spruce, working in the Amazon region of Brazil, did somewhat better, collecting a number of new species. In Central America few collectors made many collections until modern times. Even Standley and Julian A. Steyermark, two of the most prodigious collectors in the region, did not make many collections of Araceae. Both gathered well over 100,000 collections in their careers. Yet in all, Standley made only 146 collections of *P.* subg. *Philodendron,* comprising 21 species in all of Central America. Of this total only 6 of the collections (these previously mentioned) proved to be undescribed species, none of which Standley recognized as new. Standley was not avoiding collecting *Philodendron* because they constituted a lot of work to press. This is demonstrated by the fact that he collected *P. radiatum* 13 times and *P. warszewiczii* 12 times. These are among the most difficult plants to prepare owing to their huge size and fleshy parts.

That so few new species of *Philodendron* were collected was apparently due to the fact that in earlier times relatively few roads led into areas of wet forest.

Matuda, working exclusively in Mexico and concentrating on Araceae, accrued 27 collections of *P.* subg. *Philodendron* and only 1 of these, *P. glanduliferum,* proved ultimately to be new to science. George Bunting, also working only in Mexico (under the numbers of Harold Moore of Cornell University), made 36 collections of *P.* subg. *Philodendron,* including 2 new species (*P. dressleri* and *P. jodavisianum*).

Steyermark, though collecting many more *Philodendron* in Venezuela later in his career, collected only 26 Central American *P.* subg. *Philodendron,* comprising 9 species, none of which were new. L. O. Williams, who also worked on the *Flora of Guatemala* and collected for many years in Guatemala, Honduras, and Costa Rica, made only 14 collections of *P.* subg. *Philodendron.* Two of these were species that remained undescribed until this work, namely *Williams 628* (*P. sulcicaule*) and *Williams 28387* (*P. wilburii* var. *longipedunculatum* Croat & Grayum). Percy Gentle, collecting in Belize, made 20 collections. The *Philodendron* subg. *Philodendron* collections of Pittier in Costa Rica totaled nine, none representing new species. Adolf Tonduz, also working in Costa Rica, made only five collections of this group. Alberto Brenes made four collections in Costa Rica between 1926 and 1932. Two of them, *P. brenesii* and *P. bakeri,* proved to be new. Paul Allen made five collections of *Philodendron* in Costa Rica, four of which were described as new (though two were subsequently synonymized). Aside from these few collections of new species mentioned above, no other new species were collected until the early 1960s. Roy Lent, living in Costa Rica and collecting between 1964 and 1971, made 24 collections of *P.* subg. *Philodendron,* including 5 new taxa. These are: *P. lentii* Croat & Grayum, *P. hederaceum* var. *kirkbridei, P. strictum, P. thalassicum* Croat & Grayum, and *P. wilburii* var. *wilburii.* W. C. Burger, collecting in Costa Rica between 1968 and 1986, in part with one-time aroid specialist Richard Baker, made 56 collections of *P.* subg. *Philodendron,* including 5 new species, *P. bakeri, P. chirripoense, P. crassispathum, P. thalassicum,* and *P. wilburii.*

Though Panama is even richer in Araceae than Costa Rica, the collecting activity there was not particularly rewarding. The *Philodendron* collections of H. von Wedel, who worked in Bocas del Toro Province in Panama, totaled only seven. Robert Woodson and his collaborators, Paul Allen, and Carrol Dodge collectively made only 11 collections before the *Flora of Panama* project was begun. This occurred in a country that proved to have 96 species, 65 new to science.

Even James Duke, who regularly got into areas of wet forest in many parts of Panama, made only four collections of *P.* subg. *Philodendron,* none of them new.

Collecting activities begun by Walter H. Lewis and staff from the Missouri Botanical Garden in the early 1960s were more aggressive by using heli-

copters, and made it into areas not previously accessible. Despite this greater penetration, even these expeditions resulted in few specimens of *Philodendron*. John Dwyer, one of the principal participants in these early Panama expeditions (and later Belize), made 14 collections of *Philodendron* (mostly from Panama), 2 of which [*P. dwyeri* (from Belize) and *P. straminicaule* Croat)] were new to science. During the same period, Edwin Tyson, while teaching for Florida State University in the former Canal Zone, made 16 collections, 5 of them new to science: *P. annulatum* Croat & Grayum, *P. dolichophyllum* Croat, *P. lazorii* Croat, *P. llanense* Croat, and *P. tysonii* Croat. Even the late Alwyn Gentry, who made more than 80,000 collections of tropical American plants during his career and who went to many remote and interesting areas, made only 24 collections of *P.* subg. *Philodendron* in Central America. Three of them, *P. llanense*, *P. pseudauriculatum*, and *P. wilburii*, were undescribed at the time.

Collecting in Honduras, Costa Rica, and Panama between 1973 and 1993, Ron Liesner collected 43 species of *P.* subg. *Philodendron*, 4 of them, *P. alticola* Croat & Grayum, *P. crassispathum*, *P. findens*, and *P. llanense*, new to science.

Michael Grayum, an aroid specialist working primarily with *P.* subg. *Pteromischum*, was involved personally or in conjunction with other collectors, in making (since 1984) 426 *Philodendron* collections (in both Central and South America). Of this total, 153 were of *P.* subg. *Philodendron* for Central America. His collections are particularly useful, since they are accompanied by excellent field notes. He was responsible for collecting 13 undescribed species of *P.* subg. *Philodendron*: *P. angustilobum* Croat & Grayum, *P. aromaticum* Croat & Grayum, *P. bakeri*, *P. brunneicaule* Croat & Grayum, *P. cotobrusense*, *P. crassispathum*, *P. cretosum* Croat & Grayum, *P. dodsonii* Croat & Grayum, *P. grayumii* Croat, *P. scalarinerve* Croat & Grayum, *P. straminicaule*, *P. thalassicum*, and *P. wilburii*.

My own collecting activities with *Philodendron* began in 1967 with work on the *Flora of Barro Colorado Island* (Croat, 1978). Collecting on BCI and taking other trips in Panama with Walter Lewis, John Dwyer, and others gave me my first real experience gathering Araceae. Many of the areas visited were not previously explored by botanists, mostly in wet or very wet areas where numerous new Araceae occurred. Many species were collected for the first time even in areas where considerable collecting had been carried out in the past. In some cases nearly all the species collected on a given day proved to be new to science. Later, when serving as the Missouri Botanical Garden's resident botanist in Panama, during 1970–1971, and while continuing my work on Barro Colorado Island, I took many field trips to other areas of Panama. By this time I had become seriously interested in collecting Araceae, and many plants were brought back to Summit Garden for cultivation and study. Upon my return to St. Louis, most of these collections were shipped to the Missouri Botanical Garden where many have persisted. In all, 3582 collections of *Philodendron* have been made by myself (or sometimes in conjunction with another collector) in Central and South America; 1715 of these were made in Central America, and 1594 of these were members of *P.* subg. *Philodendron*: these Central American collections represented 52 undescribed species.

FOSSIL HISTORY

The fossil history of the Araceae was reviewed recently by Grayum (1990). The records are scant and inconclusive, but macrofossils of Araceae showed the family to be relatively diverse by the early Tertiary (Daghlian, 1981; Gregor & Bogner, 1984), and at least four modern subfamilies were present by the Oligocene. No fossil pollen definitely ascribed to *Philodendron* has yet been encountered (Grayum, 1990). A plant fossil from Tennessee believed to be a *Philodendron*, and described as *P. limnestis* Dilcher & Daghlian (Dilcher & Daghlian, 1977), has proven to be a member of Peltandreae, either *Peltandra* or *Typhonodorum* (J. Bogner, pers. comm.). This fossil was believed by the authors to be a member of *P.* subg. *Meconostigma*; Mayo (1991) discussed in detail why he believed that it could not be a *Philodendron*, instead comparing it most closely with *Typhonodorum*.

Intrageneric Relationships

The last thorough taxonomic revision of the Araceae was that by Engler (1905–1920), conducted in part by K. Krause (Engler & Krause, 1908, 1920; Krause, 1913). That revision included eight subfamilies of Araceae with *Philodendron* in its own subfamily and tribe, Philodendroideae and Philodendreae, respectively. Philodendreae (Engler, 1911) shared the subfamily with seven other tribes, namely, Schismatoglottidinae, Anubiadeae, Aglaonemateae, Dieffenbachieae, Zantedeschieae, Typhonodoreae, and Peltandreae. Engler (1912) grouped *Philodendron* with *Homalomena* and the genera of the largely Asian subtribe Schismatoglottidinae (*Bucephalandra*, *Gamogyne*, *Microcasia*, and *Piptospatha*) into subtribe Philodendrineae.

Bogner and Nicolson (1991) left Engler's subfamily Philodendroideae intact, but Grayum (1984) made substantive changes including an incorporation of the subfamily Calloideae and the Calocasioideae (thus forcing a change in the subfamilial name to Calloideae, because of nomenclatural priority). The subfamily is divided into *Nephthytis*, *Aglaonema*, *Peltandra*, and *Philodendron* Alliances. In Grayum's system, *Philodendron*, in its own tribe Philodendreae, originally shared the alliance with the tribes Spathicarpeae, Dieffenbachieae, and Bognereae. Both *Dieffenbachia* and *Bognera* are in their own tribes, but the Spathicarpeae have eight small genera mostly occurring in southern South America: *Asterostigma*, *Gearum*, *Gorgonidium*, *Mangonia*, *Spathantheum*, *Spathicarpa*, *Synandrospadix*, and *Taccarum*. Grayum (1990) later placed *Philodendron* close to Homalomeninae and the African genera *Culcasia* and *Cercestis* (which had been placed in the Pothoideae and Lasioideae, respectively, by Engler). They all share similar stem and stamen vasculature as well as extrafloral nectaries and resin canals in their roots and a sclerotic root hypodermis. Most (excluding Homalomeninae) also lack an anther endothecium that is present in all other Araceae (Grayum, 1990). Grayum believed that the Philodendroideae are a sister group to the Pothoideae (including Engler's Monsteroideae), which have in common the exclusive characteristics of geniculate petioles, cork formation in aerial roots, compound vascular bundles, collateral bundles, and other features (Grayum, 1984).

While there is reasonable agreement on the classification of tribes and subtribes, subfamilial concepts are still evolving. A comparison of the major systems of classification at the suprageneric level was made by Croat (1990[1992]). It included the systems of Hotta (1970), Grayum (1990), and Bogner and Nicolson (1991).

Phenetic analysis on the Philodendroideae by Mayo (1986) shows *Philodendron* to be distinct but without any definitive diagnostic features with which to distinguish it completely from other genera. He reported the genus to be only distantly related to other genera in the subfamily but that its closest relatives were the African genera *Culcasia* and *Cercestis*. In his survey of sclerotic hypodermis in the roots of Araceae, French (1987a) provided evidence to link *Philodendron* to the West African genera *Anubias*, *Culcasia*, and *Cercestis* and the neotropical *Montrichardia*.

More recently, in an attempt to bridge differences in the systems of Bogner and Nicolson, Grayum, and Hay and Mabberley (1991), Mayo et al. (1995) conducted another sweeping survey and produced a cladistic analysis. While maintaining essentially the same alliances suggested by Grayum (1990), Mayo et al. (1995) placed all araceous genera with unisexual flowers in subfamily Aroideae. *Philodendron* is placed in tribe Philodendreae in the *Philodendron* Alliance, along with tribe Homalomeneae with *Furtadoa* and *Homalomena* and tribe Anubiadeae (*Anubias* only). Their cladistic analysis also shows *Bognera* to be a close ally of *Dieffenbachia*.

Another cladistic analysis resulting from a study of chloroplast DNA restriction site variation in the Arifloraе by French et al. (1995) places *Philodendron* as a sister group to *Homalomena*, suggesting, according to Grayum (1996), that Homalomeninae is paraphyletic. According to French's findings, *Anubias* is a sister taxon of *Homalomena*, *Furtadoa*, and *Philodendron* taken together, while *Montrichardia* is a sister taxon to all four of these genera.

While questions still remain about the closest generic relatives of *Philodendron*, the classification by Mayo et al. (1995) has taken into account all the evidence to date including the extensive molecular studies by French.

The genera of Araceae most easily confused with *P.* subg. *Philodendron* are *Homalomena* and *Dieffenbachia*, with *Schismatoglottis* coming a distant third. Despite the somewhat more distant placement of *Dieffenbachia* from *Homalomena*, herbarium material of *Dieffenbachia* is most easily confused with *Philodendron*, sometimes requiring the opening of the spathe to determine the genus. Since the pistillate flowers of *Dieffenbachia* are distant from one another, surrounded by clavate staminodia and borne on a spadix that is fused throughout its length to the spathe, while those of *Philodendron* are closely compacted, devoid of staminodia, and borne on a spadix that is largely free from the spathe, separation from *Dieffenbachia* is immediate as long as the flowers are visible. Dried sterile material without field notes denoting terrestrial habit (consistently true of *Dieffenbachia*, but rarely so of *Philodendron*) or scent (usually foul and of oxalic acid in *Dieffenbachia*) are much more problematic. *Dieffenbachia* leaf blades are rarely ovate and never truly cordate, whereas this blade shape is common in *Philodendron*. *Philodendron* may, however, have blade shapes that closely match those of some *Dieffenbachia*. If the petiole is well preserved the presence of the petiole sheath is the best means to separate *Dieffenbachia* and *P.* subg. *Philodendron*; the latter generally has a very short sheath, while it is rare that the sheath of *Dieffenbachia* does not extend to the middle or above the middle of the petiole.

Live material of neotropical *Homalomena* is not easily confused with *Philodendron* because the for-

mer usually has anise-scented sap, while *Philodendron* usually has a distinct turpentine-like aroma, sometimes also like fresh carrots, but never anise-scented. *Philodendron* and *Homalomena* may have similar leaves, but the latter often has pubescence on the blades and pubescence and/or scales and spines on the petioles. These two genera have similar inflorescences with unisexual flowers, sterile and fertile sections of the staminate portion of the spadix, and a close arrangement of pistillate flowers, not to mention the similar constricted spathe that persists after anthesis. However, *Homalomena* can usually be determined by the presence of minute, club-shaped staminodia sparsely scattered among the pistils.

Sterile specimens of neotropical *Schismatoglottis* may be confused with *Philodendron* by the novice because the two genera share similar venation. However, *Schismatoglottis* always occurs terrestrially, often in somewhat marshy situations where *Philodendron* rarely occurs. In fertile condition they are easily separated by the spathe promptly dehiscing above the tube in *Schismatoglottis*, with the staminate portion of the spadix falling free. By contrast, in *Philodendron* the spathe is thick and persistent, usually reclosing over the staminate portion of the spadix, which in turn rots away inside, never really falling free until the spathe opens in fruit.

Sterile material of *Spathiphyllum* has been confused with *Philodendron*, but that genus differs by its consistently terrestrial habit, long-sheathed petioles (exhibited in *Philodendron* only in *P.* subg. *Pteromischum*), the presence of trichoscherieds, and by its distinctive, closely spaced primary lateral veins.

Infrageneric Relationships

Philodendron is currently divided into three subgenera. A subgeneric system of classification for *Philodendron* was proposed as early as 1832 by Schott, who recognized four unranked groups: *Euphilodendron*, *Calostigma*, *Meconostigma*, and *Sphincterostigma*. The latter two were combined by Engler (1899) as *P.* subg. *Meconostigma*. Schott's *Calostigma* was later called *P.* sect. *Oligospermium* Engl. (Engler, 1878) and is once more called *P.* sect. *Calostigma* [(Schott) Pfeiffer] (Mayo, 1990). *Euphilodendron* became *P.* sect. *Polyspermium* in Engler's *Flora Brasiliense* treatment in 1878 and must now be treated according to the Code (Greuter et al., 1994) as *P.* sect. *Philodendron* (Mayo, 1990).

It was not until Kunth's (1841) treatment that members of what are now called *P.* subg. *Pteromischum* were removed from *Monstera* and placed in *Philodendron*. Schott recognized *Pteromischum* as a grex in his 1860 *Prodromus*, and Engler first recognized the species occurring in this group as *P.* sect. *Pteromischum* in his *Flora Brasiliensis* treatment (Engler, 1878).

Phylogenetic and phenetic analyses by Mayo (1986, 1988) have shown *Philodendron* to have three subgenera distinct in vegetative and floral morphology, floral anatomy, and to some extent by distribution. *Philodendron* subg. *Meconostigma*, with a predominantly southeastern South American distribution, is highly apomorphic but cladistically primitive in the genus (Mayo, 1990). Based on a study of gynoecial morphology Mayo considers *P.* subg. *Meconostigma* to have evolved in eastern Brazil as a group adapted to open habitats and later spread into the more humid Amazon basin. By the same standard he assumed that *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* also arose later and became predominant as hemiepiphytes in humid forests. He considered *P.* subg. *Pteromischum* to be a sister group to *P.* subg. *Philodendron* and that *P.* subg. *Philodendron* is the most advanced of the three subgenera. The geological history of the continent would probably support this since eroded mountain plateaus of eastern Brazil are much older than the current land surfaces of the Amazonian basin. Most of the species of the genus, now so rich on the Andean slopes of northern and western South America, surely must have evolved since the Andes arose during the late Cenozoic.

Mayo elevated *P.* sect. *Pteromischum* to the status of subgenus (Mayo, 1989) and Grayum (1996) subdivided the subgenus into two sections, *P.* sect. *Pteromischum* (Schott) Engl. with sylleptic[4] sym-

[4] *Sylleptic shoots* are shoots that develop from lateral meristems without any cessation of activity after initiation, i.e., growth is continuous with the lateral shoot usually taking over from the main axis, which terminates in flowering in most Araceae genera. *Sylleptic sympodial growth*, characteristic of *P.* subg. *Philodendron*, results when branching occurs from a non-resting lateral bud such that the existing stem with its terminal inflorescence is immediately overtopped by continued growth of the axillary branch in a manner that makes it appear that the growth of the stem is indeterminate and that the inflorescences produced appear to be axillary to the leaf produced by the new stem segment. This type of growth, though in reality a series of branches, each with a single cataphyll (prophyll of Ray), a single stem segment, and a single leaf (sympodial foliage leaf of Ray; metaphyll of Grayum) and terminated by an inflorescence, appears to be an unbranched stem producing a continuous series of cataphylls, and a continuous series of what appears to be laterally attached leaves each with an axillary inflorescence (see fig. 3 in Ray, 1987b).

podial growth and *P.* sect. *Fruticosa* Grayum with proleptic[5] sympodial growth (Ray, 1987b), a growth form that is rare in the family, known only in *Alocasia* and a few species of *Monstera* (Grayum, 1996).

Philodendron subg. *Philodendron* is difficult to define and is primarily distinguished by its negatives, i.e., it lacks the specific characteristics of *P.* subgenera *Pteromischum* and *Meconostigma* (see key to subgenera below). There are relatively few members of *P.* subg. *Philodendron* with a pachycaulous habit common to so many members of *P.* subg. *Meconostigma,* i.e., with very stout, generally erect stems and possessing conspicuous leaf scars. *Philodendron* subg. *Philodendron* also lacks the conspicuous, more or less triangular scales borne in the leaf axils of *P.* subg. *Meconostigma.* Though sometimes obvious (Fig. 11) in *P.* subg. *Philodendron,* they are usually small and inconspicuous and fall early. The species most similar to *P.* subg. *Meconostigma* is *P. warszewiczii,* but another species, *P. basii,* is similar in being large with a thick, erect stem.

Species of *P.* subg. *Pteromischum* have subtle characteristics that to the expert permit immediate recognition. These characters include the slender, somewhat woody, brittle stem, a conspicuous petiole sheath, thinner blades with rather pronounced primary lateral veins, the presence of interprimary veins, and the frequent presence of raphide cells or stitch-like markings. Another feature that is often useful in separating *P.* subg. *Pteromischum* from *P.* subg. *Philodendron* is the much higher incidence of asymmetrical leaf blades in the former. Species with asymmetrical (especially at the base) blades are not common in *P.* subg. *Philodendron.* Some species of *P.* subg. *Philodendron* may have oblong to elliptic, non-cordate blades like those of *P.* subg. *Pteromischum,* but they never have the fully sheathed petioles of the latter (except in juvenile condition, which may confuse the non-expert).

The three subgenera of *Philodendron* in general can be most easily separated by the characters presented in the following key (modified after Mayo, 1991).

KEY TO THE SUBGENERA OF *PHILODENDRON*

1a. Stem of mature flowering plants with a succession of many leaves terminated by a solitary or commonly several inflorescences; petioles with long sheaths narrowly encircling the stem at their base ..... *P.* subg. *Pteromischum*

1b. Stem of mature flowering plants with a succession of short sympodial segments each bearing a cataphyll and a single leaf with the inflorescence(s) 1 to many and appearing to be borne in the leaf axils; petioles of adult plants with short, usually inconspicuous petiole sheath and borne on the side of the stem, not encircling it at the base.

2a. Stems often arborescent; staminodial zone between staminate and pistillate zones of the spadix subequal or longer than fertile zone; stamens usually at least 3 times longer than broad ..... *P.* subg. *Meconostigma*

2b. Stems rarely arborescent, often scandent; staminodial zone between staminate and pistillate zones of spadix much shorter than the fertile staminate zone; stamens less than 3 times longer than broad ..... *P.* subg. *Philodendron*

There are also a number of anatomical characteristics separating the subgenera. Vegetative buds of *Philodendron* subg. *Philodendron* are always located below the point of overlap in the sheath margins of the cataphyll, whereas they are lacking in *P.* subg. *Pteromischum* (Ray, 1987b). *Philodendron* subg. *Pteromischum* is distinct in having a style with a shallow compitum[6] with a subepidermal concentration of raphide crystals (Mayo, 1986, 1989) and a total lack of tannin cells in the stamens (Mayo, 1986). In addition, while hypophyllous[7] stem segments are typical for *P.* subg. *Philodendron* they are ambiphyllous,[8] hyperphyllous,[9] or peraphyllous[10] in *P.* subg. *Pteromischum. Philodendron* subg. *Philodendron* is characterized by having continuous parenchyma from the cortex to the center of the stem. In contrast, *P.* subg. *Pteromischum* has a central cylinder with a solid ring of fibers around it.

While not definitive, there are a number of other features that normally are useful to separate *P.*

[5] *Proleptic sympodial growth,* characteristic of members of *Philodendron* sect. *Fruiticosa* (Grayum, 1996), results when branching occurs from a bud that has rested, relative to the parent shoot, so that the lateral branch does not appear until well after the inflorescence has set fruit and fallen off. Thus the inflorescence appears to be terminal, not axillary as in sylleptic sympodial growth. The first few internodes in proleptic growth are very short, lack buds, and produce a consecutive series of cataphylls or reduced leaves (see fig. 2 in Ray, 1987b).

[6] The common depression that leads to individual stylar canals.

[7] Hypophyllous stem segments are those those in which the petiole scar borders the lower edge of the segment (see figs. 3, 7 in Ray, 1987b).

[8] Ambiphyllous stem segments are so short that the petiole scars border on both ends of the stem segment (see figs. 9–11 in Ray, 1987b).

[9] Hyperphyllous stem segments have the petiole scar at the upper edge of the stem segment (see figs. 2, 8 in Ray, 1987b).

[10] Peraphyllous stem scars are those in which the internode subtending the petiole "is elongated and supercedes the point of attachment" (Ray, 1987b).

subg. *Pteromischum*. Its blades are typically more or less oblong, moderately thin, and typically more inequilateral than those of *P.* subg. *Philodendron*. The stems of *P.* subg. *Pteromischum* are commonly less than 1 cm in diameter and frequently with rather long internodes. While there are many members of *P.* subg. *Philodendron* with more or less oblong leaf blades, blades of most species are cordate or subcordate at the base. Many members of *P.* subg. *Pteromischum* have stems that branch and spread away from their support before flowering; this behavior is rare in *P.* subg. *Philodendron*.

Because of the usually conspicuously sheathed petioles of *P.* subg. *Pteromischum*, the subgenus is more likely to be confused with sterile specimens of *Rhodospatha* than with the oblong-bladed species of *P.* subg. *Philodendron* (and in such cases the presence of trichosclereids beneath the epidermis of *Rhodospatha* easily distinguishes it from *Philodendron*).

Relationships within *P.* subg. *Philodendron*

Discussion of subgeneric classification. Any attempt to revise the subgeneric classification of *Philodendron* subg. *Philodendron* is frustrated by the lack of morphological characteristics that correlate with one another throughout the subgenus. Engler (1899) separated the species of *P.* subg. *Philodendron* primarily on the basis of leaf shape, leaf blade venation, and the nature of the pistil (i.e., number of locules per ovary, type of placentation, and number of ovules per locule). Most sections, all moderately small ones, were separated on the basis of leaf morphology. These are: *P.* sect. *Tritomophyllum*, *P.* sect. *Schizophyllum*, and *P.* sect. *Polytomium*. Two sections, *P.* sect. *Macrogynium* and *P.* sect. *Camptogynium*, are based on the nature of the pistil. Following a cladistic analysis of a relatively small number of species, including some in *P.* subg. *Philodendron*, Mayo (1986) concluded that *Philodendron* should be divided into two to three sections instead of the existing nine sections in the genus. While I agree that *P.* sect. *Macrolonchium* should be reduced, I think that a cladistic analysis making use of the leaves as well would justify the existence of the remaining sections recognized by Krause with the possible exception of *P.* sect. *Camptogynium*, which was not studied by Mayo.

The most time-honored way to separate species in *P.* subg. *Philodendron* is based on number of ovules per locule, a system first devised by Engler stemming from his first revision of *Philodendron* (Engler, 1878). Engler used the number of ovules per locule to separate two large groups, which he called *P.* sect. *Polyspermium* and *P.* sect. *Oligospermium* (now *P.* sect. *Philodendron* and *P.* sect. *Calostigma*, respectively). These two sections together comprise the largest percentage of species in the subgenus. As they are constituted they are very diverse morphologically, and it is possible that the number of ovules per locule will not prove to be reliable for separation at the sectional level. It is possible that species with relatively few ovules or solitary ovules may have evolved independently several times from ancestors with numerous ovules having axile placentation. Since it has not yet been determined if this is the case, the classification system used here will in general be conservative.

Krause (1913) closely followed Engler's sectional revision. His *P.* sect. *Philodendron* (as *P.* sect. *Polyspermium*) consisted of species with axile placentation and "many" ovules per locule, while *P.* sect. *Calostigma* (as *P.* sect. *Oligospermium*) consisted of those species with sub-basal (or less frequently basal) placentation with "1 or few" ovules per locule. Since the time of the last revision of *Philodendron* many species have been added, and the distribution of ovules per locule for all species now forms a more complete continuum. There is still a significant correlation between axile placentation and moderately large numbers of ovules per locule and the converse, basal and sub-basal placentation and relatively low numbers of ovules. Both *P.* sect. *Philodendron* and *P.* sect. *Calostigma* will be discussed below.

While these two groups, *P.* sect. *Philodendron* and *P.* sect. *Calostigma*, constitute the largest percentage of Central American species, several other sections are separated on the basis of leaf shape, venation, and style type (see above key). Each of these will be discussed in turn, despite the fact that some do not occur in Central America. Krause (1913) treated ten sections in his revision of *Philodendron*. As previously discussed, *P.* sect. *Pteromischum* has been elevated to the status of subgenus, and *P.* subg. *Macrolonchium* Engl. has been reduced to a subsection of *P.* subg. *Philodendron*.

1. **Philodendron** sect. **Baursia** (Rchb. ex Schott) Engl., in Mart., Fl. bras. 3(2): 134. 1878. *Philodendron* grex *Baursia* Rchb. ex Schott, Syn. Aroid. 73. 1856. TYPE: *Philodendron crassinervium* Lindl. (lectotype, designated by Mayo, 1990).

As defined by Engler and Krause, *P.* sect. *Baursia* consists of species with generally inconspicuous primary lateral veins, but the group as constituted

by Krause remains highly variable in terms of its ovules, habit, and leaf shape. The group comprises species with moderately many ovules and axile placentation, moderately many ovules with basal placentation, a few ovules with basal placentation, and solitary ovules with basal placentation. All of these species have leaves purportedly devoid of primary lateral veins. In reality this is not true of all species included in the group. Most species have elongate, simple blades, but three have 3-lobed or tripartite blades.

With 33 species included by Krause the section was third in size of the three major sections (*P.* sect. *Philodendron* with 64 and *P.* sect. *Calostigma* with 53 species). One species, *P. acreanum* K. Krause, is actually a member of *P.* sect. *Pteromischum.* Of the remaining species in the section, those that best fit the description of the group occur principally in eastern South America and in the upper Amazon basin and have more or less oblong leaf blades. *Philodendron crassinervium* is the type of the section. Except for *P. crassinervium, P. longilaminatum* Schott (with axile placentation), *P. bahiense* Engl., and *P. paxianum* K. Krause (each with solitary ovules per locule), species of *P.* sect. *Baursia* have a few basal ovules per locule and oblong to oblong-elliptic blades. Many but not all have indistinct primary lateral veins.

Some members of Krause's *P.* sect. *Baursia,* especially the species that are vines with a solitary ovule per locule and occur in the Andes west of the Continental Divide, such as *P. lehmannii* Engl., *P. ellipticum* Engl., *P. pachycaule* K. Krause, *P. chimboanum* Engl., *P. longipes* Engl., and *P. graveolens* Engl., do not seem to belong with the remainder and should perhaps be put into another section. The same is true of the three-lobed and tripartite species, *P. deltoideum* Poepp. & Endl., *P. panduriforme* (Kunth) Kunth (Krause also included here *P. reichenbachianum* Schott, now a variety of *P. panduriforme*), and *P. micranthum* Poepp. ex Schott. With the exception of *P. micranthum,* which has primary lateral veins lacking or weak, these species have primary lateral veins at least some of the time (though they are indistinct in *P. deltoideum*). None of the three species appear to have any other features in common with the more typical members of *P.* sect. *Baursia,* e.g., *P. crassinervium* Lindl., *P. linnaei* Kunth, and *P. callosum* K. Krause, among others.

Mayo (1986) believed that *P.* sect. *Baursia* contained two groups of species, and he would also separate *P. deltoideum* and related species from the remainder, suggesting that Schott's grex *Oligophlebium* be recognized to accommodate these species.

Some species that were placed in *P.* sect. *Baursia* will have to be reinvestigated to determine if they belong instead in *P.* sect. *Philopsammos* G. S. Bunting (1986). That group is often similar in having elongated leaf blades, but it differs in having bilocular ovaries whereas those of *P.* sect. *Baursia* are plurilocular.

By no means all of the species with more or less oblong blades in *P.* sect. *Baursia* have primary lateral veins weak or lacking. At least one species, *P. wendlandii,* the only Central American species placed in *P.* sect. *Baursia* by Engler, should be placed in *P.* sect. *Calostigma.* It has distinct primary lateral veins and a spongiose petiole with a distinct dark green annular ring like the other members of *P.* subsect. *Glossophyllum* in Central America. This leaves Central America without members of *P.* sect. *Baursia.*

2. Philodendron sect. **Philopsammos** G. S. Bunting, Phytologia 60: 306. 1986. TYPE: *Philodendron ptarianum* Steyerm., Fieldiana, Bot. 28: 99. 1956. [*Philodendron callosum* K. Krause subsp. *ptarianum* (Steyerm.) G. S. Bunting, Phytologia 64: 467. 1988.]

Philodendron sect. *Philopsammos* is restricted to South America, known largely from the region of the Guiana highlands with extensions into the Amazon basin, occurring principally on white sand savannas, sandstone outcrops, and on tepuis, rarely in alluvium in lowland forests. It is characterized by having usually terrestrial or epipetric, thick, creeping stems with mostly short internodes, mostly long persistent, mostly intact cataphylls, moderately long petioles, mostly erect, geniculate petioles, more or less oblong, elliptic to narrowly ovate, coriaceous blades, usually lacking any prominent posterior lobes and with usually distinct, sometimes moderately obscure primary lateral veins. Inflorescences are moderately large with pistils bilocular, rarely 3-locular, and ovaries moderately numerous with axile placentation.

Included in the section are the following species: *P. canaimae* G. S. Bunting, *P. craspedodromum* R. E. Schult., *P. dunstervilleorum* G. S. Bunting, *P. dyscarpium* R. E. Schult., *P. peraiense* G. S. Bunting, *P. phlebodes* G. S. Bunting, *P. pimichinense* G. S. Bunting, *P. callosum* K. Krause, *P. pulchrum* G. M. Barroso, *P. remifolium* R. E. Schult., *P. sabulosum* G. S. Bunting, *P. steyermarkii* G. S. Bunting, and *P. tatei* K. Krause. Perhaps also to be included

in this group is *P. englerianum* Steyerm. No species in the group occur in Central America.

In describing this section Bunting (1986) made no mention of how the section is distinguished from *P.* sect. *Baursia* (or any other section). This is a critical point since both sections have species with elongated blades and at least sometimes have primary lateral veins not markedly more prominent than the interprimary veins (secondary lateral veins). The section is presumably distinguished from *P.* sect. *Baursia* on the basis of having mostly two locules per ovary. As an indication of its affiliation with *P.* sect. *Baursia,* Bunting, at the time he described *P.* sect. *Philopsammos,* specifically mentioned *P. callosum* (a species included by Krause in *P.* sect. *Baursia* and initially considered by Bunting to be distinct from *P. ptarianum*) as being a possible member. *Philodendron ptarianum* has proven to be closely related to *P. callosum,* but that species was described by Krause as being "plurilocula," i.e., with many locules per ovary and "pauciovulata," i.e., with few ovules per locule. If this is true, the single character separating *P.* sect. *Philopsammos* from *P.* sect. *Baursia,* namely the small number of locules per ovary, would break down even in two subspecies (as now recognized by Bunting, 1995), one of which is the type of *P.* sect. *Philopsammos.* One collection of *P. callosum, Davidse & Miller 27269,* had 2-locular ovaries with 8–10 ovules per locule with unusual black, shiny seeds. It would clearly appear to be a member of *P.* sect. *Philopsammos.*

3. Philodendron sect. **Philodendron.** TYPE: *P. grandifolium* (Jacq.) Schott

Philodendron sect. *Philodendron* in Central America is both large and diverse, and like *P.* sect. *Calostigma* (a discussion of which follows) it is further subdivided here into subsections.

With 38 species (40 taxa) *P.* sect. *Philodendron* is the second largest section in *P.* subg. *Philodendron* in Central America. *Philodendron* sect. *Philodendron* is characterized by having axile placentation and typically many ovules per locule but, owing to its size and diversity, there are no other characters that completely characterize the group. *Philodendron* sect. *Polyspermium* (according to the Code (Art. 21) it must now be *P.* sect. *Philodendron*) was subdivided by Krause into six groups, "Gruppen" (termed subsections by Mayo, 1990). These subsections will be discussed here, especially in relation to the Central American species.

SUBSECTIONS OF *P.* SECT. *PHILODENDRON*

1. Philodendron subsect. **Macrolonchium** (Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *Philodendron* grex *Macrolonchium* Schott, Prodr. syst. Aroid. 269. 1860. TYPE: *Philodendron simsii* (Hook.) G. Don (lectotype, designated by Mayo, 1990: 64).

This is a small group of species characterized by D-shaped or broadly and sharply sulcate petioles and the presence of short stems with short internodes. The leaf blades typically are ovate-triangular. The cataphylls typically persist as fibers. The ovaries are 5–10-locular with numerous ovules per locule. This group was treated by Engler (1899) and Krause (1913) as a section based on stems with internodes shorter than broad versus scandent stems, but the group is in no way warranted at the sectional level based on this or any other character.

Though neither short stems nor D-shaped petioles are unique to this group, it appears to be natural at the subsectional level. All of the species have similar ovate-triangular blades and coarse reddish brown persistent cataphyll fibers. The two pinnately lobed species in the group, *P. pinnatifidum* (Jacq.) Schott and *P. robustum* Schott, seem unlikely members of this subsection. Those species are very similar to *P. fendleri* K. Krause, which Engler placed in his *P.* sect. *Polytomium. Philodendron pinnatifidum* and *P. robustum* should probably be placed there as well. They seem to have little in common with the other simple-leaved species. *Philodendron melinonii* Brongn., *P. fragrantissimum, P. simsii,* and *P. roraimae* K. Krause all appear to be related. The only Central American species in this subsection is *P. fragrantissimum.*

2. Philodendron subsect. **Canniphyllum** (Schott) Mayo, J. Linn. Soc., Bot. 100. 168. 1989. *Philodendron* grex *Canniphyllum* Schott, Syn. Aroid. 76. 1856. TYPE: *Philodendron fibrillosum* Poepp.

This is a small group that included only five species in Krause's revision and one of these, *P. coerulescens,* proved to be a synonym of *P. inaequilaterum,* a member of *P.* subg. *Pteromischum. Philodendron juninense* Engl., *P. fibrillosum,* and *P. cuneatum* Engl. are all Andean species, while the no doubt distantly related *P. blanchetianum* Schott is a species from eastern Brazil in Bahia. *Philodendron* subsect. *Canniphyllum* has only a few species in Central America. Both *Philodendron cretosum* and *P. roseospathum* have persistent fibrous cataphylls and resemble the type species, *P. fibril-*

losum (selected by Mayo, 1990). The only other Central American species that has characteristics to fit in the subsection is *P. chirripoense*, which is tentatively placed here, though it differs in having longer, more slender internodes and lacks persistent cataphylls. The presence or absence of persistent cataphylls is highly correlated with the length of internodes (persistent when internodes are short, deciduous when internodes are long) and thus it is not surprising that *P. chirripoense* would lack cataphylls. Still, the latter is a most peculiar species so its placement remains in doubt.

3. Philodendron subsect. **Platypodium** (Schott) Engl., in Mart., Fl. bras. 3: 137. 1878. *Philodendron* grex *Platypodium* Schott, Syn. Aroid. 85. 1856. TYPE: *Philodendron pterotum* K. Koch & Augustin (lectotype, designated by Mayo, 1990: 61).

This group was characterized by Schott (1856) as having D-shaped petioles. While he included both *P. pterotum* and *P. fragrantissimum*, Engler later transferred the latter to his *P.* sect. *Macrolonchium* (Schott) Engl. Mayo (1990) designated the only remaining species in Schott's section, namely *P. pterotum*, as the type species.

In addition to *P. pterotum*, Krause (1913) placed in *P.* sect. *Platypodium* four more species, *P. clementis* Wright, now considered a synonym of *P. fragrantissimum* (a member of *P.* subsect. *Macrolonchium*); *P. splitgerberi* Schott, a possible synonym of *P. fragrantissimum*; *P. lechlerianum* Schott, a close relative of *P. purpureoviride* (a member of *P.* subsect. *Solenosterigma*); and *P. ernestii* Engl. Thus, of the species listed by Krause, probably only *P. pterotum* and *P. ernestii* belong here. It is unlikely that *P. ernestii* is very closely related to *P. pterotum*, but it does appear to be closely related to *P. brunneicaule*, another species placed in this section.

In addition to *P. pterotum*, other species of *P.* subsect. *Platypodium* that occur in Central America are: *P. brunneicaule*, *P. copense*, *P. findens*, and *P. fortunense* Croat.

4. Philodendron subsect. **Psoropodium** (Schott) Engl., in Mart., Fl. bras. 3: 138. 1878. *Philodendron* grex *Psoropodium* Schott, Syn. Aroid. 84. 1856. TYPE: *Philodendron ornatum* Schott (lectotype, designated by Mayo, 1990: 61).

As defined by Schott (1856), this is a group that has petioles verrucose at the apex. Mayo (1991) appropriately selected *P. ornatum* as the lectotype. Krause's description, "petioles semirounded above, smooth or asperous, blade base cordate or sagittate," would accommodate more than half of the species in the genus *Philodendron*, but Schott's intention for the subsection was clear. The only other species included by Schott was *P. rubens* Schott, now considered by some authors to be a synonym of *P. ornatum*. Krause also expanded the group substantially, adding a number of plants that do not have glandular petioles and others that have proven to be synonyms of *P. ornatum*. The latter are: *P. muschlerianum* K. Krause, *P. dolosum* Schott, *P. asperatum* K. Koch, and *P. tobagoense* Engl. The aberrant elements which, I believe, are unrelated to *P. ornatum* include *P. brevilaminatum* Schott and *P. traunii* Engl. (now both synonyms of *P. fragrantissimum* in *P.* subsect. *Macrolonchium*), *P. grandipes*, and *P. maximum* K. Krause, a gigantic species from the southwest Amazon basin that is unlikely to be related in any way to *P. ornatum*. I have moved *P. grandipes* from *P.* subsect. *Psoropodium* to *P.* subsect. *Philodendron*, where it more appropriately belongs.

Krause also included in his *Psoropodium* group three other poorly known species, *P. thaliifolium* Schott, *P. brandtianum* K. Krause, and *P. bertae* K. Krause. These do not appear to be in any way related to *P. ornatum*. It is clear from these as well as the other species included by Krause that the section as defined by Engler and by Krause no longer resembles Schott's original description. Probably a number of the species will need to be moved into other groups, or the section will need to be more well defined. As currently defined no species in *P.* subsect. *Psoropodium* occur in Central America.

5. Philodendron subsect. **Solenosterigma** (Klotzsch ex Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *Philodendron* grex *Solenosterigma* Klotzsch, Syn. Aroid. 81. 1856. TYPE: *Philodendron scandens* K. Koch & Sello [(= *Philodendron hederaceum* (Jacq.) Schott (lectotype, designated by Mayo, 1990: 61)].

As treated by Krause (1913), this appears to be a natural group, consisting of *P. hederaceum*, the type, as well as *P. consanguineum* Schott and a number of relatives. *Philodendron fuertesii* K. Krause, *P. krebsii* Schott, and *P. urbanianum* K. Krause all closely resemble *P. consanguinem*, and *P. marginatum* Urb., *P. prieurianum* Schott, *P. oxycardium*, *P. micans*, and *P. melanochrysum* Linden & André are all synonyms or subspecies of *P. hederaceum*. These species share long, slender inter-

nodes, deciduous, mostly unribbed cataphylls, more or less terete petioles, ovate-cordate leaf blades, and solitary inflorescences.

Other species included by Krause in *P.* subsect. *Solenosterigma* are *P. purpureoviride* (aside from *P. hederaceum* and *P. brevispathum*, the only other species of the group that occurs in Central America), *P. jenmanii* K. Krause, and *P. scabrum* K. Krause. The latter two species are now considered synonyms of *P. muricatum* Willd. ex Schott. Though surely belonging in *P.* subsect. *Solenosterigma* (along with the two synonyms already placed here) Krause placed *P. muricatum* in *P.* sect. *Calostigma*.

Philodendron brevispathum is transferred here from *P.* subsect. *Cardiobelium* (Schott) Engl., since it appears to be closely related to *P. muricatum*.

6. **Philodendron** subsect. **Philodendron**

Philodendron grex *Cardiobelium* Schott, Syn. Aroid. 88. 1856. *Philodendron* subsect. *Cardiobelium* (Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *Philodendron* "Gruppe" *Cardiobelium* (Schott) Engl., Bot. Jahrb. Syst. 26: 522, 529. 1899. TYPE: *Philodendron giganteum* Schott (lectotype, designated by Mayo, 1990: 60).

Philodendron grex *Eubelium* Schott, Syn. Aroid. 92. 1856. *Philodendron* subsect. *Eubelium* (Schott) Engl., in Mart., Fl. bras. 3: 140. 1878. TYPE: *Philodendron grandifolium* (Jacq.) Schott.

As defined by Schott (1860), grex *Cardiobelium* consisted of a single species, *P. giganteum*. The group was greatly expanded by Engler (1899) and by Krause (1913) as a subgroup within section *Polyspermium*. Now with 20 species, it constitutes the largest subsection in *P.* sect. *Philodendron*. The characterization, as expanded by Krause, "petioles smooth or lightly striate, asperate; blade cordate to sagittate, with the primary lateral veins much more conspicuous than the secondary veins," is so broad that many unrelated species might easily be contained within it. Certainly to be excluded is *P. rubens* Schott (now a synonym of *P. ornatum* and the core species in *P.* subsect. *Psoropodium*). Among the well known and seemingly distinct taxa included by Krause are *P. grandifolium*, *P. acutatum* Schott, and *P. fraternum* Schott, all with deciduous cataphylls, and *P. tenue*, *P. schottianum*, and *P. panamense*, with persistent cataphylls. The type, *P. giganteum*, also has conspicuous persistent cataphylls. A particularly unusual species included by Krause is *P. quitense* Engl., with deeply three-lobed leaves. It is probably a synonym of *P. acuminatissimum* Engl. in *P.* subsect. *Doratophyllum*.

The only Central American species included in the section by Krause were: *P. brevispathum*, *P. panamense*, *P. schottianum*, and *P. tenue*. *Philodendron brevispathum*, with its scaly stems, is best accommodated with *P. muricatum* in *P.* subsect. *Solenosterigma*.

Philodendron subsect. *Philodendron* has 20 species in Central America. The size and diversity of *P.* subsect. *Philodendron* warrant the recognition of the five series presented below.

SERIES OF *P.* SUBSECTION *PHILODENDRON*

1. **Philodendron** ser. **Philodendron.** TYPE: *P. grandifolium* (Jacq.) Schott

The series is not known from Central America, but has several species in South America. This group is characterized by thick stems, deciduous cataphylls, subterete petioles, large ovate-triangular blades conspicuously lobed at the base, several inflorescences per axil, and 5–7-locular ovaries with many ovules per locule. In addition to the type, *P. acutatum* Schott, *P. billietiae* Croat, and *P. megalophyllum* Schott appear to be typical members of this group, having many ovules per locule, deciduous cataphylls, more or less terete petioles, and ovate-triangular leaf blades.

2. **Philodendron** ser. **Impolita** Croat, ser. nov. TYPE: *P. strictum* G. S. Bunting

Internodia brevia; cataphylla persistentia; petiolus teres vel D-formatus; lamina palida adaxialiter, glaucescens.

Etymology. From impolitus meaning unpolished, i.e., matte, in reference to the matte and pale lower blade surfaces.

Three Central American taxa, *P. hebetatum*, *P. strictum*, and *P. thalassicum*, and at least one additional undescribed species from South America belong in this group. It is characterized by having leaf blades dark to medium green above but very pale, almost white beneath and covered with a minute waxy covering making the surface matte. The species have relatively short internodes, persistent cataphylls that often dry yellowish or have patches of yellowish epidermis persistent (not always true for *P. thalassicum*). Petioles may be obtusely somewhat flattened to D-shaped and dry with a yellowish epidermis (not always true for *P. thalassicum*). Blades are ovate-cordate to ovate-triangular.

3. **Philodendron** ser. **Velvetina** Croat, ser. nov. TYPE: *P. gigas* Croat

Internodia brevia, maxime crassa; cataphylla D-formata, persistentia in fibris tenuibus; petiolus subteres; lamina ovata-cordata, bicolorata, velutina adaxiliter, impolita abaxialiter, 81–125 cm longa, 37–90 cm lata.

Etymology. From velutinus meaning velvet, referring to the velvety upper surfaces of the blades.

The subsection consists of a single species, *P. gigas*, in Central America but would also include *P. andreanum* Devansaye from northern Colombia. The group is characterized by its stout stems, short internodes, cataphylls that persist as thin fibers, subterete petioles, and especially by the very large, narrowly ovate-cordate blades, which are velvety and bicolored on the upper surface with the midrib and primary lateral veins paler, and paler and matte on the lower surface. Inflorescences range up to 7 per axil.

4. Philodendron ser. **Fibrosa** Croat, ser. nov. TYPE: *P. jodavisianum* G. S. Bunting

Internodia brevia, cataphylla persistentia ut fibrae; petiolus plerumque teres aut subteres; lamina ovato-cordata; pistilla cum placentatione axiali; loculi pluriovulati.

Etymology. Fibrosa = composed of separable fibers, in reference to the cataphylls persisting as fibers.

This represents the largest series in *P.* subsect. *Philodendron.* It is characterized by thick stems, short internodes, cataphylls that usually persist as a mass of fibers on the stem, usually subterete petioles, and more or less ovate-cordate blades. Pistils have axile placentation and many ovules per locule.

The following species of *P.* ser. *Fibrosa* occur in Central America: *P. alticola, P. antonioanum, P. breedlovei, P. chiriquense, P. dodsonii, P. grandipes, P. jodavisianum, P. lazorii, P. llanense, P. panamense, P. pirrense, P. purulhense, P. scalarinerve, P. schottianum,* and *P. tenue.* Of these a few are still doubtful. *Philodendron grandipes,* with a D-shaped petiole, and *P. jodavisianum,* with a U-shaped petiole, perhaps belong in *P.* subsect. *Platypodium* but also do not seem to be related to the species in that group. *Philodendron breedlovei,* which appears to lack persistent cataphylls (specimen very incomplete), is at odds with the other species but fits nowhere else. A few species are in related clusters within the series; for example, *P. lazorii* and *P. panamense* seem to be closely related as do *P. grandipes* and *P. jodavisianum.*

Grayum (pers. comm.) believes that *P. dodsonii* perhaps belongs with *P. pterotum* in *P.* subsect. *Platypodium.*

5. Philodendron ser. **Albisuccosa** Croat, ser. nov. TYPE: *P. albisuccus* Croat

Internodia brevia; succus albus, calcareus; cataphylla persistentia in fibris tenuibus pallidis; petiolus subteres; lamina ovato-cordata; inflorescentia solitaria; pistilla 5–6-locularia; loculi cum 18–20 seminibus.

Etymology. Albus = white; succus = juice, sap, in reference to the white sap of cut parts.

The series consists of a single species, *P. albisuccus,* characterized by having copious white sap, which turns chalky on drying. Only one other species in Central America, *P. cretosum,* shares this unusual feature. It may belong in the same series despite its linear to oblanceolate leaf blades. It currently is placed in *P.* subsect. *Canniphyllum.*

7. Philodendron subsect. **Achyropodium** (Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *P.* grex *Achyropodium* Schott, Syn. Aroid. 85. 1856. TYPE: *P. verrucosum* L. Mathieu ex Schott

This is a seemingly quite natural group characterized by scaly petioles. As defined by Schott (1856) it was represented only by the type, *P. verrucosum.* Krause (1913) included six species (one of which, *P. arcuatum* K. Krause, is a synonym of *P. brevispathum* in *P.* subsect. *Solenosterigma*). The others in the subsection are: *P. nanegalense* Engl., *P. pilatonense* Engl., and *P. gualeanum* Engl. (all of which, I believe, represent a single species), as well as *P. serpens* Hook. f. All but *P. verrucosum* were known only from South America. There are several other undescribed species in *P.* subsect. *Achyropodium* now known from South America.

Philodendron subsect. *Achyropodium* is largely restricted to the northern Andes and lower Central America (Costa Rica and Panama) but has one species, *P. verrucosum,* that ranges as far south as Peru. The subsection is represented in Central America by *P. glanduliferum* subsp. *glanduliferum, P. hammelii, P. malesevichiae, P. squamicaule, P. squamipetiolatum,* and *P. verrucosum.*

4. Philodendron sect. **Calostigma** (Schott) Pfeiffer, Nomencl. Bot. 2: 674. 1874. *P.* [rankless] b. *Calostigma* Schott, in Schott & Endl., Melet. Bot. 19. 1832. TYPE: *P. imbe* Schott

Philodendron sect. *Calostigma* is the largest section in Central America with 48 species comprising 52 taxa. It is characterized by having basal or subbasal placentation and typically solitary or few ovules per locule. Owing to its size and diversity, there are no other characters that completely characterize the group.

There are some differences between *P.* sect. *Philodendron* and *P.* sect. *Calostigma* in Central America that are statistically significant, even if not without exception. For example, 81% of those spe-

Table 1. Leaf blade breakdown by section. # = number of species.

	Blades entire								Blades not entire		
	With basal lobes				Lacking basal lobes						
	Cordate		Subcordate		Ovate		Oblong		Incised-lobate		
Section	#	% of sect.	#	% of sect.	#	% of sect.	#	% of sect.	#	% of sect.	Section total
Calostigma	28	56%	7	14%	1	2%	14	28%	0	0%	50
Macrogynium	1	100%	0	0%	0	0%	0	0%	0	0%	1
Philodendron	34	81%	3	7%	1	2%	3	7%	1	2%	42
Polytomium	0	0%	0	0%	0	0%	0	0%	3	100%	3
Tritomophyllum	3	38%	0	0%	0	0%	0	0%	5	63%	8

cies in *P.* sect. *Philodendron* have cordate blades, while only 7% have subcordate blades, and 12% lack posterior lobes. In contrast, *P.* sect. *Calostigma* has only 56% of its species with cordate blades, 14% have subcordate blades, and 30% lack posterior lobes. See Table 1 for a complete breakdown by section.

See other comparisons between *P.* sect. *Calostigma* and *P.* sect. *Philodendron* under sections entitled "Ovary Locule Number" and "Ovules Per Locule" as well as in Appendix 2, Technical Data on Pistils.

Philodendron sect. *Calostigma* was subdivided by Krause into five groups (termed subsections by Mayo, 1990). These subsections will be discussed here, especially in relation to the Central American species.

1. Philodendron subsect. **Macrobelium** (Schott) Engl., in Mart., Fl. bras. 3: 143. 1878. *P.* grex *Macrobelium* Schott, Syn. Aroid. 96. 1856. TYPE: *P. sagittifolium* Liebm.

Philodendron subsect. *Belocardium* (Schott) Engl., in Mart., Fl. bras. 3: 141. 1878. *P.* grex *Belocardium* Schott, Prodr. Syst. Aroid. 255. 1860. TYPE: *P. advena* Schott (lectotype, designated by Mayo, 1990).

As reported by Krause, *Philodendron* subsect. *Macrobelium* was the largest subsection in *P.* sect. *Calostigma*, with 22 species. It was poorly defined by Krause as consisting of species with somewhat spongy petioles, 6–12-locular ovaries with relatively few ovules per locule, and basal to sub-basal placentation. In addition (although not stated by Krause), the blades are all cordate, sagittate, or hastate. Although Krause described the subsection as having 2–5 ovules per locule, many more species have been added to the group since the last revision and several species that logically belong in *P.* subsect. *Macrobelium* have more than 10 ovules per locule, despite having sub-basal placentation.

Philodendron subsect. *Belocardium* must be synonymized with *P.* subsect. *Macrobelium* since *P. advena*, clearly a close relative of *P. sagittifolium*, was designated the lectotype of the former subsection, and Schott's definition of grex *Macrobelium* differs little from grex *Belocardium*, primarily since the blades are described as elongate-sagittate with 6–7 primary lateral veins instead of ovate-cordate blades with 3–4 primary lateral veins for grex *Belocardium*. As defined originally by Schott (1860), *P.* grex *Belocardium* comprised vining plants with ovate-cordate blades with the posterior rib mostly lacking and not at all naked along the sinus and bearing solitary inflorescences with 1–2 ovules per locule. The group consisted of *P. subovatum* Schott (= *P. advena*), *P. hoffmannii* (= *P. hederaceum*), *P. deviatum* Schott (= *P. jacquinii*), *P. advena*, *P. populneum* K. Koch, *P. erubescens* Linden, *P. jacquinii*, *P. lindenii* Schott, *P. acrocardium* Schott, and *P. consanguineum* Schott. Several of these species are now known to be synonyms of *P.* sect. *Oligocarpidium* or *P.* sect. *Macrogynium*. *Philodendron lindenii* would have better served as a lectotype for the group and, along with *P. erubescens*, *P. deviatum*, and *P. populneum*, might have to be formed into a group distinct from *P.* sect. *Belocardium*.

Engler (1913) synonymized Schott's grex *Glossophyllum* with *P.* "Gruppe" *Belocardium*, but the former group, as defined by Schott, appears to be distinct and will be resurrected in this work. It comprises more or less scandent plants with tumid petioles and more or less oblong blades that are frequently subcordate or cordulate at the base (see that section for more details).

Because of its size (28 species) and the diverse composition of the species comprising *P.* subsect. *Macrobelium*, it was deemed necessary to divide the subsection into four series. A discussion of the new series of *P.* subsect. *Macrobelium* follows.

1. Philodendron ser. **Macrobelium** (Schott) Croat, ser. nov. TYPE: *P. sagittifolium* Liebm.

Philodendron ser. *Macrobelium* is the largest group of species in *P.* subsect. *Macrobelium* and includes the type. *Philodendron* ser. *Macrobelium* is distinguished by having moderately coriaceous, cordate to sagittate blades with the basal posterior rib usually not naked or only weakly naked near its base. In addition, cataphylls are usually deciduous or only briefly persistent. Most of the species in the series have a strong resemblance to the widespread *P. sagittifolium.* All members have type D styles (see section on style type), relatively few ovules per locule (usually 1–5, rarely to 6, 7, or 8). In most cases the ovules are contained within a translucent or transparent ovule sac.

Central American representatives of *P.* ser. *Macrobelium* are: *P. advena, P. annulatum, P. aromaticum, P. coloradense, P. dwyeri, P. edenudatum, P. ferrugineum, P. grayumii, P. knappiae, P. mexicanum, P. platypetiolatum, P. sagittifolium, P. subincisum, P. sousae, P. verapazense,* and *P. zhuanum. Philodendron platypetiolatum* is unusual in having a much-flattened petiole. Perhaps it warrants recognition as a separate series.

Philodendron mexicanum, long considered a member of the group, is unusual in not greatly resembling *P. sagittifolium* and in having blades sometimes more or less hastate.

It is possible that *P. annulatum* belongs in *P.* subsect. *Glossophyllum* because it sometimes has a purple annular ring at the apex of the petiole (one of the features characterizing this subsection) and usually has only 1–2 ovules per locule (though sometimes 4–5 ovules per locule).

2. Philodendron ser. **Ecordata** Croat, ser. nov. TYPE: *P. brenesii* Standl.

Internodia elongata vel brevia; cataphylla decidua; petiola subteres; lamina acuta vel subcordata ad basim; nervia minores saepe "etched" in superficie supra; pistila 5–14 locularia; loculi plerumque 4–14 ovulati.

Philodendron ser. *Ecordata* represents a group of species with elongate stems, internodes often longer than broad, deciduous cataphylls, elongate petioles, and blades that are ovate to ovate-elliptic, acute, or at most subcordate at the base (hence the name "ecordata," meaning without a cordate blade), often with the minor veins on the upper surface weakly etched. The basal veins are either free to the base or if they are united into a posterior rib, the latter is not naked or is naked for only a short distance. Pistils are 5–14-locular and locules are 4–14-ovulate.

The Central American species of *P.* ser. *Ecordata* are: *P. brenesii, P. crassispathum, P. davidsonii, P. lentii,* and *P. niqueanum.* A relationship between *P. brenesii* and *P.* ser. *Impolita* is possible, based on the glaucous lower blade surface in *P. brenesii,* but no other member of the group has glaucous leaves. Moreover, all the members of the above group usually have internodes longer than wide and have deciduous, rather than persistent cataphylls.

3. Philodendron ser. **Reticulata** Croat, ser. nov. TYPE: *P. tysonii* Croat

Internodia brevia; cataphylla persistentia in fibris tenuibus; petiolus lamina subequans aut longior, teres aut subteres; lamina ovato-cordata; pistila cum loculis 5–9-ovulatis; ovulae plerumque 5–7 per ovaria.

Etymology. Reticulus, meaning netted, referring to the dried network of cataphyll fibers characterizing this series.

Philodendron ser. *Reticulata* is the only group of species in *P.* subsect. *Macrobelium* with a few ovules per locule, stems with short internodes, and persistent cataphylls. Most species with short internodes and persistent cataphyll fibers are members of *P.* sect. *Philodendron.* Species in this group have terete or subterete petioles about as long as the ovate-cordate blades and pistils with 5–9 locules, each with 5–7 ovules.

Philodendron ser. *Reticulata* is represented in Central America by only two species, *P. jefense* and *P. tysonii.*

4. Philodendron ser. **Pachycaulia** Croat, ser. nov. TYPE: *P. basii* Matuda

Caudex succulentus; internodia brevia, crassa; cataphylla 2-costata, persistentia intacta; petiolus teres; lamina ovato-cordata, costae postice desnudae secus sinum ad 4 cm; pistila 4–6-locularia; loculi 4–6 ovulati.

Etymology. Pachy = thick, caule = stem, referring to the thick, succulent stems.

Philodendron ser. *Pachycaulia* is represented by a single species and is characterized by its very stout succulent stems with intact persistent cataphylls, terete petioles, ovate-cordate blades with the posterior rib naked along the sinus to 4 cm. The pistil has a type D style and is 4–6-locular with 4–6 ovules per locule. It is believed that the succulent stems evolved to store water, allowing the plant to survive the long dry season in western Mexico. The series is represented only by *P. basii* from western Mexico.

2. Philodendron subsect. **Glossophyllum** (Schott) Croat, comb. nov. Basionym: *Philodendron* grex *Glossophyllum* Schott, Syn. Aroid. 80. 1856. TYPE: *P. elaphoglossoides* Schott (lectotype, designated by Mayo, 1990).

1. Philodendron ser. **Glossophyllum** Croat, ser. nov. TYPE: *P. elaphoglossoides* Schott

Philodendron subsect. *Glossophyllum* consists of two new series, *Glossophyllum* and *Ovata.*

Philodendron ser. *Glossophyllum,* as defined here, has the appearance of being a natural group of species with more or less oblong leaves acute or frequently cordulate or subcordate at the base. The primary lateral veins are usually distinct. Stems are typically somewhat scandent, though some members of the group, such as *P. auriculatum, P. bakeri, P. dolichophyllum, P. ligulatum, P. morii, P. pseudauriculatum, P. utleyanum,* and *P. wendlandii,* sometimes have the internodes scarcely longer than broad. The petioles are usually spongy or subspongy, usually subterete, and often bear a purplish or greenish annulus around the circumference where the petiole joins the blade; the cataphylls may be unribbed or sharply 1–2-ribbed and are typically deciduous (though persisting for a time in some species with short internodes, e.g., *P. auriculatum* and *P. wendlandii*). The style type is variable in the group, with most having B or D type styles but with one species, *P. granulare,* having an unusual type E style. Many species in the series have orange berries. *Philodendron* ser. *Glossophyllum* ranges from Nicaragua to Colombia and Ecuador on the Pacific slope and to the Guianas and the Amazon basin.

Krause included this group of plants with his section *Belocardium,* comprising both Schott's grex *Belocardium* and grex *Glossophyllum.* The former group consisted of plants with elongate internodes and ovate-cordate to sagittate blades, and Krause included *P. subovatum* Schott (= *P. advena*), *P. lindenii* Schott, *P. weberbaueri* Engl., *P. smithii, P. subhastatum* Engl. & K. Krause, *P. myrmecophyllum* Engl., *P. pachyphyllum* K. Krause, *P. advena,* and *P. viride* Engl. The latter group included species with mostly oblong blades. He characterized his section *Belocardium* as having tumid petioles and unilocular ovaries. Most of the species in the cordate-bladed group are not believed to be closely related to *P.* ser. *Glossophyllum* and have been referred here to *P.* subsect. *Macrobelium* (see discussion of *P.* subsect. *Macrobelium*). What remains is a group that usually has more or less oblong blades with tumid petioles that are purple-ringed at the apex and ovaries usually unilocular.

Philodendron smithii, the only other Central American species among those mentioned above, does indeed have tumid petioles and only a single ovule per locule like most members of *P.* subsect. *Glossophyllum,* but the great difference in leaf shape in this species and others placed here warrant their separation into another series within *P.* subsect. *Belocardium* (see below).

Though Krause's revision characterized *P.* subsect. *Belocardium* as having a single ovule per locule, that is not in itself the defining feature of the subsection. For example, several species typical of the group have oblong leaves, purple-ringed petioles, and the same general appearance but have more than one ovule per locule. These are: *P. auriculatum,* with (3)4 ovules per locule; *P. ligulatum* var. *heraclioanum,* and *P. ligulatum* var. *ovatum,* both with 2; *P. pseudauriculatum,* with 1–2(4); and *P. wendlandii,* with 2. *Philodendron bakeri* sometimes has 2 ovules per locule. Other Central American species, each with 1 ovule per locule are *P. brewsterense, P. correae, P. dolichophyllum, P. folsomii, P. granulare, P. immixtum, P. ligulatum, P. morii, P. ubigantupense,* and *P. utleyanum.*

Typical South American species in *P.* subsect. *Glossophyllum* presented by Krause (1913) are: *P. cyrtocleum* Diels (= *P. ruizii* Schott), *P. longipetiolatum* Engl., *P. heterophyllum* Poepp., *P. uleanum* Engl., *P. adhatodifolium* Schott, *P. elaphoglossoides* Schott, *P. ruizii* Schott (erroneously placed in sect. *Baursia* by Schott), *P. wittianum* Engl., and *P. angustialatum* Engler. *Philodendron tenuipes* Engl., placed in *P.* subsect. *Belocardium* by Engler, appears to be closely related to *P. fibrillosum* Poepp. and probably belongs in *P.* subsect. *Canniphyllum.*

Other species of *P.* subsect. *Glossophyllum* described since the last revision by Krause are *P. acutifolium* K. Krause, *P. buntingianum* Croat, *P. liesneri* Croat, and *P. wurdackii* G. S. Bunting.

Though, as defined here, *P.* subsect. *Glossophyllum* ser. *Glossophyllum* consists only of species with more or less oblong blades, some of the species are somewhat anomalous. *Philodendron granulare* is much like other species in *P.* subsect. *Glossophyllum,* but it has a style that is unique in the group (Style Type E; see discussion of this under that species). *Philodendron brewsterense* and *P. ubigantupense* are still poorly known but appear to belong here. Perhaps the most doubtful is *P. dolichophyllum,* with 3–7 ovules, which is certainly high for this group; however, it is otherwise similar in most aspects to other members of the subsection. *Philodendron wendlandii,* placed by Krause in *P.* sect.

Baursia, seems to fit best in *P.* subsect. *Glossophyllum*. It differs from other members of subsection *Glossophyllum* in having a petiole that is usually broader than thick and sharply flattened adaxially and lacks an annular ring.

2. Philodendron ser. **Ovata** Croat, ser. nov. TYPE: *P. smithii* Engl.

Caudex longus vel brevis; internodia plerumque longiora quam lata; cataphylla plerumque decidua; petioli subaequantes laminam, teres vel subteres, cum annulo deficienti apice; lamina ovata vel ovato-triangulata, cordata vel sagittata ad basi; pistilla cum stylo plerumque "type B," rare C; ovaria 4–8-locularia; loculi uniovulati aut raro 2–5.

Philodendron ser. *Ovata* is a somewhat heterogeneous group characterized by blades ovate to ovate-triangular and cordate to subcordate at the base, with terete or subterete petioles lacking an annular ring at the apex. Locule number varies from 4 to 8, and each usually has a single ovule. Berry color is greenish white to white, yellowish to lavender for most species known, but *P. cotonense* and *P. wilburii* have orange fruits. Though only seven Central American species are known, the series undoubtedly has South American representatives.

The relationship with other members of *P.* subsect. *Glossophyllum* is uncertain. Aside from the usually solitary ovule per locule and usually somewhat spongy petiole, there is little resemblance between this group and typical members of *P.* subsect. *Glossophyllum*, which have elongated, rather than more or less ovate, blades. *Philodendron dominicalense* is the most doubtful member of the group; with the strongest possible similarity to *P. dodsonii* except for having a solitary ovule per locule (rather than about 20 ovules per locule as in *P. dodsonii*), it would appear that it might belong elsewhere. *Philodendron cotonense*, despite having 4–5 ovules per locule, appears also to belong to this section, considering its marked resemblance to *P. wilburii* and even *P. smithii*.

Central American species of *P.* ser. *Ovata* are: *P. cotonense*, *P. dominicalense*, *P. microstictum*, *P. smithii*, *P. straminicaule*, *P. sulcicaule*, and *P. wilburii*. With the exception of *P. smithii*, which ranges from Mexico to Nicaragua, *P.* ser. *Ovata* in Central America ranges from Nicaragua to Panama.

3. Philodendron subsect. **Oligocarpidium** (Engl.) Mayo, J. Linn. Soc., Bot. 100: 168. 1989. TYPE: *P. multispadiceum* Engl. (lectotype, designated by Mayo, 1990).

As defined by Krause, this was a group of four species that differed greatly from one another. *Philodendron deviatum* Schott has proven to be a synonym of *P. jacquinii* (which was placed by Krause in its own *P.* sect. *Macrogynium*). Another species that he included, *P. pittieri*, is just poorly preserved material of *P. hederaceum*, which Krause placed in his *P.* "Gruppe" *Solenosterigma* in *P.* sect. *Philodendron*. This leaves only *P. multispadiceum* Engl. and *P. muricatum* which, in my opinion, are quite unrelated. *Philodendron muricatum* is the oldest name for two other synonyms, *P. jenmanii* K. Krause and *P. scabrum*, which were placed by Krause in *P.* subsect. *Solenosterigma*. Though I am doubtful of the affinity between *P. hederaceum* and *P. muricatum*, it seems best to include *P. muricatum* in subsect. *Solenosterigma* because *P. muricatum* is clearly a member of *P.* sect. *Philodendron* and not *P.* sect. *Calostigma*.

This leaves only *P. multispadiceum*, which Mayo (1990) wisely chose as the type of *P.* subsect. *Oligocarpidium*. There are two Central American representatives of the subsection and a number of other undescribed South American species as well. The Central American species are *P. clewellii* and *P. heleniae*.

The subsection is distinguished by having a relatively large number of small (usually 4–10 cm long) inflorescences per axil. The plants are vines with long internodes and long-petiolate, narrowly ovate to ovate-cordate blades that have the basal veins either lacking or all free to the base and without the development of a posterior rib. Both Central American species represented have a type B style and an ovule sac surrounding the ovules.

4. Philodendron subsect. **Bulaoana** Mayo [as "*Bulaoanum*"], J. Linn. Soc., Bot. 100: 168. 1989. TYPE: *P. bulaoanum* Engl. (lectotype, designated by Mayo, 1989).

This subsection includes two species treated by Krause, *P. bulaoanum* and *P. acuminatissimum*. They probably represent the same species, a plant with deeply 3-lobed leaves and persistent, reddish brown cataphyll fibers. Currently the subsection is known only from South America. Krause treated this subsection as *P.* "Gruppe" *Doratophyllum*, but that name has no priority at the subsectional level (Mayo, 1990).

This subsection can be easily confused with and is perhaps inseparable from *P.* sect. *Tritomophyllum*. A moderately large number of South American species, including *P. barrosoanum* G. S. Bunting, *P. cataniapoense* G. S. Bunting (Bunting placed it in *P.* "Gruppe" *Doratophyllum*), *P. effusilobum*

Croat, *P. holtonianum* Schott, *P. hylaeae* G. S. Bunting (*P.* sect. *Calostigma*), *P. levelii* G. S. Bunting (similar to *P. barrosoanum*), *P. panduriforme* Schott, and *P. victoriae* G. S. Bunting might all belong here.

Philodendron subsect. *Bulaoana* and *P.* sect. *Tritomophyllum* are separated on weak features. Krause described his "Gruppe" *Doratophyllum* as having somewhat succulent petioles longer than the blade, a hastate blade, and ovaries that are several-ovulate near the base of the locule, whereas he described *P.* sect. *Tritomophyllum* as having tripartite blades with the lateral lobes erect or spreading, and the primary lateral veins more prominent than the minor veins. The ovary was described as 5–11-locular with the locules 1- or more-ovulate. The Central American species that appear to be closely related have one or two ovules per locule, whereas those of *P.* subsect. *Bulaoana* are described as having several ovules per locule. These distinctions are pretty weak, and further study of the members of both groups is necessary to decide whether the two groups should be merged.

5. Philodendron subsect. **Eucardium** (Engl.) Mayo, J. Linn. Soc., Bot. 100: 168. 1989. *Philodendron* "Gruppe" *Eucardium* Engl., Bot. Jahrb. Syst. 26: 535, 542. 1899. TYPE: *P. wallisii* Regel ex Engl.

This is a subsection of dubious status, based only on *P. wallisii*. The original description characterizes the subsection as having scarcely succulent petioles that are flattened to sulcate abaxially, cordiform blades, and 5–6-locular ovaries with a few sub-basal ovules per locule. Unfortunately, *P. wallisii* is a poorly known taxon for which, so far as is known, no material is extant.

Following his treatment of *Eucardium*, Krause discussed several poorly known species, all of which lacked inflorescences and for which no proper sectional placement was possible. Among these were *P. andreanum*, which is almost certainly related to *P. gigas*, a member of *P.* ser. *Velutina*. Listed among these dubious species are *P. latilobum* Schott and *P. obtusilobum* Miq. The former is a synonym of *P. panduriforme*, possibly a member of *P.* subsect. *Bulaoana*, which it most resembles. *Philodendron obtusilobum* is a poorly known species of unknown origin, known only from a single leaf. Its affinities remain unclear, but it appears similar to *P. lindenii* Schott or *P. rubens* Schott.

Also described among this group of unassigned species were *P. gloriosum* André and *P. mamei* André. These two species, along with *P. sodiroi* Hort., appear to be closely related and probably constitute a new section. *Philodendron pastazanum* K. Krause has similar features and probably belongs here as well. Another species known from the Amazonian lowlands of Peru and believed to be new is also in this group. All the species in this putative new section are terrestrial plants with a unique growth form for *Philodendron*. All have a short, repent, creeping stem with erect leaves clustered near the apex. The internodes are usually much broader than long and have cataphylls persistent, sometimes persisting somewhat intact. The petioles are frequently winged or undulate-winged along adaxial margins (but not *P. gloriosum*) and blades are typically quite attractive, sometimes mottled with paler green, sometimes (as in *P. gloriosum*) somewhat velvety. The group is restricted to South America chiefly in the upper Amazon region. Studies of the ovules are necessary to confirm these speculations, and investigations will be carried out as material becomes available.

5. Philodendron sect. **Tritomophyllum** (Schott) Engl., in Mart., Fl. bras. 3: 144. 1878. *Philodendron* grex *Tritomophyllum* Schott, Syn. Aroid. 107. 1856. *Baursia* sect. *Tritomophyllum* (Schott) T. Post & Kuntze, Lex. gen. phan. 63. 1903. TYPE: *P. tripartitum* (Jacq.) Schott (lectotype, designated by Mayo, 1990: 63).

The section is distinguished by having a scandent habit, three-lobed leaf blades and 1–2 ovules per locule. The section ranges from Mexico to South America, ranging as far as Ecuador on the Pacific slope and to Venezuela, the Guianas, and the Amazon basin. It is represented in Central America by six species: *P. angustilobum*, *P. anisotomum*, *P. cotobrusense*, *P. madronense*, *P. rothschuhianum* (Engl. & K. Krause) Croat & Grayum, and *P. tripartitum*. In South America there are a number of species with 3-lobed leaves, including: *P. barrosoanum*, *P. cataniapoense*, *P. effusilobum*, *P. holtonianum*, *P. hylaeae*, *P. levelii*, *P. panduriforme*, and *P. victoriae*, all now tentatively placed in *P.* subsect. *Bulaoana*, which might belong in *P.* sect. *Tritomophyllum*. Certainly *P. hylaeae*, with 1–2 ovules per locule and a strong similarity with *P. tripartitum*, would appear to be closely related to *P.* sect. *Tritomophyllum*.

Bunting (1986) placed *P. cataniapoense* in *P.* sect. *Oligospermium* "Gruppe" *Doratophyllum* (now *P.* subsect. *Bulaoana*) but this species has a single ovule per locule, elongate internodes, and deciduous cataphylls. It may properly belong with *P.* sect. *Tritomophyllum*.

Some of the above-mentioned South American species are doubtfully included here, since they

have several (more than 1 or 2) ovules per locule. *Philodendron levelii* has 2–4 sub-basal ovules, and *P. barrosoanum* has 4–6 ovules attached above the base. *Philodendron victoriae* is apparently closely related to *P. barrosoanum* so it probably has similar ovules. It is possible that none of these species belong to *P.* sect. *Tritomophyllum*, but on the other hand they do not closely match *P. bulaoanum*, the type of *P.* subsect. *Bulaoana*, either.

6. Philodendron sect. **Schizophyllum** (Schott) Engl., in Mart., Fl. bras. 3: 144. 1878. *Philodendron* grex *Schizophyllum* Schott, Syn. Aroid. 104. 1856. TYPE: *P. pedatum* (Hook.) Kunth (lectotype, designated by Mayo, 1990: 63).

The section is a small but natural group of 6–7 scandent species with irregularly pedatisect leaves, 3–4 ovules per locule, and sometimes scaly petioles, primarily restricted to eastern South America and the Amazon basin, but with one species, *P. pedatum*, more widespread and ranging to northwestern Colombia. The species may occur in Central America, according to horticulturist John Hall of Costa Rica, who illustrated such a plant supposedly from the Osa Peninsula. Characteristically, no material was collected and this claim cannot be refuted.

7. Philodendron sect. **Polytomium** (Schott) Engl., in Mart., Fl. bras. 3: 145. 1878. *Philodendron* grex *Polytomium* Schott, Syn. Aroid. 108. 1856. TYPE: *P. radiatum* Schott (lectotype, designated by Mayo, 1990: 63).

The section is a small group of 7–8 species with pinnately or bipinnately lobed leaves from the West Indies, Central America, and northern South America. Plants are vines or appressed climbers with more or less terete petioles, generally deeply lobed, large, moderately coriaceous blades, and flowers with several axillary or sub-basal ovules per locule. Only one species, *P. distantilobum* K. Krause, was reported for the Amazon basin, but another species, *P. pinnatifidum*, placed erroneously, I believe, in *P.* sect. *Macrogynium*, really belongs here as well. It is also a species occurring in the upper Amazon basin. Two additional species, *P. angustisectum* Engl. and *P. elegans* K. Krause, occur in Colombia. *Philodendron fendleri* occurs in Trinidad and northern Venezuela, and *P. lacerum* (Jacq.) Schott occurs in the Greater Antilles (Cuba, Jamaica, and Hispaniola). One poorly known species, *P. houlettianum* Engl., has been reported from French Guiana but no material exists to confirm what it is. The most widespread species in the section, *P. radiatum*, occurs in Central America, ranging from Mexico (San Luis Potosí) to Colombia (Antioquia). *Philodendron radiatum* var. *pseudoradiatum* is endemic to the State of Chiapas in Mexico. Central American species in *P.* sect. *Polytomium* are *P. warszewiczii*, ranging from Mexico to Nicaragua, and *P. dressleri*, which is endemic to Mexico.

Mayo (1986), following a cladistic survey of inflorescence types, concluded that *P. fendleri* belonged in a group with *P. melinonii* and *P. pedatum*. Based on overall morphology I would conclude that the three species are not closely related. The latter is, in my opinion, a member of a distinctive section, *P.* sect. *Schizophyllum*. *Philodendron melinonii* Brongn., a distinctive species with cordate blades and placed by Krause in *P.* sect. *Macrolonchium*, is in my opinion, not related to either of the sections with lobed leaves.

8. Philodendron sect. **Macrogynium** Engl., Bot. Jahrb. Syst. 26: 553. 1899. TYPE: *P. hoffmannii* Schott.

Philodendron sect. *Macrogynium* is one of two small sections treated by Krause (1913) (the other being *P.* sect. *Camptogynium*). *Philodendron* sect. *Macrogynium* consists of a single species, *P. jacquinii* (treated by Krause as *P. hoffmannii*). Both sections are represented by scandent species, distinguished by having the style prolonged and much narrower than the ovary and a single ovule per locule. Despite these similarities the two sections are very different from one another. *Philodendron jacquinii* (*P.* sect. *Macrogynium*) has setose stems and thin, veiny, ovate-cordate blades which may be deciduous during the dry season. Its spathe is bulbous and roomy inside, quite unlike most species. The style, though narrowed to the apex, has a typical, hemispheroid stigma. For differences with *P.* sect. *Camptogynium*, see below.

Philodendron brevispathum, with its similarity to *P. jacquinii*, might be considered a relative, but the former has branched scales, not simple trichomes on stems and petioles; a normal, sessile style; and 6–14 ovules per locule with axile placentation, rather than 2 ovules per locule and sub-basal placentation for *P. jacquinii*.

This section appears, at least on the surface, to be natural. No other species known is alike either morphologically or ecologically. Its thin, veiny leaves are deciduous in the dry season and the large colorful infructescences are prominently displayed in a mostly deciduous environment.

9. Philodendron sect. **Camptogynium** K. Krause in Engl., Das Pflanzenreich IV. 23Db (Heft 60): 3, 127. 1913. TYPE: *P. longistilum* K. Krause

In contrast to *P. jacquinii,* which has setose stems and thin cordate blades with prominent veins, *P. longistilum* (*P.* sect. *Camptogynium*) has glabrous stems and oblanceolate, subcoriaceous blades with obscure primary lateral veins. The chief reason for its status as the only member of a section is the peculiar prolonged style, which is deflected to one side and has a cupular apex. It is perhaps not as unique as Krause assumed. Other species are now known to have prolonged styles deflected to one side, among them two undescribed species with cordate blades from western Ecuador, one based on *Camp 3701* and the other on *Jaramillo et al. 25449.* However, neither has a cupular style apex. These perhaps represent another section, or more likely Krause's *P.* sect. *Camptogynium* may have to be incorporated in *P.* sect. *Calostigma,* where it might be easily accommodated.

KEY TO THE SECTIONS AND SUBSECTIONS OF *P.* SUBG. *PHILODENDRON*

1a. Pistils usually 2-locular, rarely 3-locular; eastern South America and Amazon basin ..... *P.* sect. *Philopsammos*
1b. Pistils 4–10-locular; throughout the range of the genus.
2a. Plants with primary lateral leaf veins moderately obscure; all South American (excludes *P. wendlandii,* which is transferred to *P.* sect. *Calostigma*) ..... *P.* sect. *Baursia*
2b. Plants with primary lateral leaf veins usually much more prominent than the minor veins.
3a. Pistil with style much narrowed and much prolonged beyond the body of the ovary and much narrower than ovary.
4a. Style turned toward apex, perpendicular to the body of the ovary; South American species only ..... *P.* sect. *Camptogynium*
4b. Style straight, directed in the same axis as the ovary; Central and South America ..... *P.* sect. *Macrogynium* (*P. jacquinii*)
3b. Pistil with style about as broad as the ovary, scarcely prolonged beyond body of ovary.
5a. Blades 3-lobed or deeply incised-lobate.
6a. Blades 3-lobed; ovules 1–3 per locule, basal or sub-basal. [Note: *P.* subsect. *Doratophyllum* with 3-lobed blades would also key here. See the discussion after that subsection.] ..... *P.* sect. *Tritomophyllum* [*P. angustilobum* (perhaps this belongs in *P.* subsect. *Macrobelium* (Schott) Engl.), *P. anisotomum, P. cotobrusense, P. madronense, P. rothschuhianum, P. tripartitum*]
6b. Blades incised-lobate; ovules 2–8 per locule, sub-basal or axile.
7a. Blades divided along the anterior lobe into two or more divisions, each division in turn terminating with much smaller lobes; petioles sometimes with trichome-like scales; South America only ..... *P.* sect. *Schizophyllum*
7b. Blades pinnately or bipinnately lobed, the divisions ± uniform along the anterior lobe; petiole never scaly; Central and South American species ..... *P.* sect. *Polytomium* [*P. dressleri, P. radiatum, P. warszewiczii*]
5b. Blades entire, sometimes with the anterior lobes markedly concave, but the blade not markedly 3-lobed or incised-lobate.
8a. Pistils with axile placentation; ovules usually 15 or more per locule, seldom with as few as 10 per locule, rarely fewer ..... *P.* sect. *Philodendron*
9a. Blades cordate to subcordate or sagittate at base; petioles various.
10a. Petioles ± D-shaped in cross section, sharply flattened adaxially, sometimes also with the lateral margins raised.
11a. Stems with internodes much broader than long ..... *P.* subsect. *Macrolonchium* (Schott) Engl. [*P. fragrantissimum*]
11b. Stems with internodes about as broad as long or longer than broad ..... *P.* subsect. *Platypodium* (Schott) Engl. [*P. brunneicaule, P. copense, P. findens, P. fortunense, P. pterotum*]
10b. Petioles terete or subterete.
12a. Petioles warty at apex; South American species (excluding *P. grandipes* erroneously placed here by Krause); *P. ornatum* Schott and relatives ..... *P.* subsect. *Psoropodium* (Schott) Engl.
12b. Petioles smooth or conspicuously scaly but not merely warty at apex.
13a. Plants scandent; internodes much longer than broad; cataphylls usually deciduous; blades cordate ..... *P.* subsect. *Solenosterigma* (Klotzsch ex Schott) Engl. [*P. brevispathum, P. purpureoviride, P. hederaceum*]
13b. Plants usually not scandent, either terrestrial or appressed-climbing with internodes broader than long or not much longer than broad; cataphylls usually persistent, rarely deciduous; blades ovate to sagittate.
14a. Plants with petioles scaly ..... *P.* subsect. *Achyropodium* (Schott) Engl. [*P. glanduliferum, P. hammelii, P. malesevichiae, P. squamipetiolatum, P. squamicaule, P. verrucosum*]
14b. Plants with petioles smooth, not scaly ..... *P.* subsect. *Philodendron*
15a. Cataphylls deciduous intact or sometimes becoming fibrous but soon deciduous ..... *P.* ser. *Philodendron* Schott [*P. giganteum* (not in Central America)]
15b. Cataphylls persisting as a mass of fibers.

16a. Blades matte on lower surface.
17a. Blades matte, not velvety on upper surface, whitish and glaucous on lower surface ..... *P.* ser. *Impolita* Croat [*P. hebetatum, P. strictum, P. thalassicum*]
17b. Blades velvety on upper surface, not whitish and glaucous on lower surface ..... *P.* ser. *Velutina* Croat [*P. gigas*]
16b. Blades usually semiglossy, never whitish or glaucous, on lower surface.
18a. Sap brown to clear, never chalky ..... *P.* ser. *Fibrosa* Croat [*P. alticola, P. antonioanum, P. breedlovei, P. chiriquense, P. dodsonii, P. grandipes, P. jodavisianum, P. lazorii, P. llanense, P. panamense, P. pirrense, P. purulhense, P. scalarinerve, P. schottianum, P. tenue*]
18b. Sap white and chalky ..... *P.* ser. *Albisuccosa* Croat [*P. albisuccus*]
9b. Blades acute to obtuse at base; petioles subterete and smooth ..... *P.* subsect. *Canniphyllum* (Schott) Mayo [*P. chirripoense, P. cretosum, P. roseospathum*]
8b. Pistils with basal or sub-basal placentation; ovules few per locule, usually fewer than 5, seldom up to 8, rarely as many as 12 (but with some locules in the same inflorescence with as few as 6 ovules per locule) ..... *P.* sect. *Calostigma*
19a. Plants usually appressed hemiepiphytic climbers; internodes frequently as long as wide or longer than wide; widespread in both Central and South America.
20a. Blades deeply 3-lobed; cataphylls persisting in a dense, reddish brown layer of fibers; South American species only; *P. acuminatissimum* Engl., *P. bulaoanum* Engl ..... *P.* subsect. *Bulaoana* Mayo
20b. Blades *not* at all 3-lobed, cordate, sagittate, or ± oblong; cataphylls deciduous or persistent, fibrous or intact; widespread in both Central and South America.
21a. Inflorescences both small and numerous, usually more than 6 per axil, less than 5 cm long ..... *P.* subsect. *Oligocarpidium* (Engl.) Mayo [*P. clewellii, P. heleniae*]
21b. Inflorescences of normal size, typically 1–few and more than 5 cm long.
22a. Pistils with several ovules per locule; petioles rarely with purple ring at apex; blades sagittate or cordate at base ..... *P.* subsect. *Macrobelium*
23a. Cataphylls deciduous.
24a. Leaf blades with minor veins not at all etched into upper surface ..... *P.* ser. *Macrobelium* (Schott) Croat [*P. advena, P. annulatum, P. aromaticum, P. coloradense, P. dwyeri, P. edenudatum, P. ferrugineum, P. grayumii, P. knappiae, P. mexicanum, P. platypetiolatum, P. sagitti-folium, P. sousae, P. subincisum, P. verapazense, P. zhuanum*]
24b. Leaf blades with minor veins etched into upper surface ..... *P.* ser. *Ecordata* Croat [*P. brenesii, P. crassispathum, P. davidsonii, P. lentii, P. niqueanum*]
23b. Cataphylls persistent.
25a. Cataphylls weathering and persisting as fibers ..... *P.* ser. *Reticulata* Croat [*P. jefense, P. tysonii*]
25b. Cataphylls persisting intact; stems markedly succulent ..... *P.* ser. *Pachycaulia* Croat [*P. basii*]
22b. Pistils with ovules solitary (or sometimes 2, as in *P. wilburii*) in each locule; petioles frequently with purple ring at apex (*P.* subsect. *Glossophyllum*); blades elongate (*P.* ser. *Glossophyllum*) or ± ovate (*P.* subsect. *Glossophyllum* ser. *Ovata*).
26a. Blades mostly ± oblong and acute to narrowly subcordate at base; petioles frequently with a purple ring at apex ..... *P.* subsect. *Glossophyllum*(Schott) Engl.; *P.* ser. *Glossophyllum* (Schott) Croat [*P. auriculatum, P. bakeri, P. brewsterense, P. correae, P. dolichophyllum, P. folsomii, P. granulare, P. immixtum, P. ligulatum, P. morii, P. pseudauriculatum, P. ubigantupense, P. utleyanum, P. wendlandii*]
26b. Blades ovate to ovate-triangular, cordate to subcordate at base; petioles usually lacking a purple ring at apex ..... P. subsect. Glossophyllum; *P.* ser. *Ovata* Croat [*P. cotonense, P. dominicalense, P. microstictum, P. smithii, P. straminicaule, P. sulcicaule, P. wilburii*]
19b. Plant habit unknown; internodes much broader than long; Colombia (exact locality unknown) ..... *P.* subsect. *Eucardium* (Engl.) Mayo

Note: For an outline of the sectional classification of *Philodendron* subg. *Philodendron* in Central America see Appendix 3.

Morphology of Vegetative Structures

Anatomy

Vegetative anatomy. (Section on Vegetative Anatomy contributed by R. C. Keating; vouchers will be cited by Keating (in press)).

General comments. *Philodendron* has secretory ducts present in all morphological parts. These occur mostly as 2–4 "files" in vascular bundles. Laticifers are of the non-anastomosing type, simple and articulated (French, 1988). The genus also has secretory ducts present in roots, stems, leaves, and inflorescences. The roots have a sclerotic hypodermis.

Leaf surfaces. Cuticle smooth or occasionally rough on both surfaces. *Epidermis*: adaxial cells polygonal (1–2:1), straight-sided. Abaxial cells similar to or larger than adaxial cells or more elongate (2–4:1 l/w). *Stomata*: abaxial, randomly oriented, brachyparacytic to brachyparahexacytic. *Venation*: secondary veins parallel with reticulate higher order veins.

Leaf Cross Section. Cuticle of medium thickness, may intrude deeply along anticlinal walls of epidermal cells. Abaxial cuticle may be thinner and smooth or striate. *Epidermal cells*: large or small, square to columnar or tile-like adaxial cells, larger abaxially, or same size; outer and inner walls flat. *Stomata* level with surface with conspicuous double cuticular flanges often present. *Hypodermis*: absent or as 1–3 layers present on adaxial side of midrib, or as isodiametric cells beneath both epidermal layers (in *P. crassispathum*, hypoderm of 1–4 layers adaxially and 2–3 layers abaxially), cells may contain dark material. *Mesophyll*: palisade 1–4 layers of elongated or rounded cells, usually packed with plastids; occupying 10–30% of lamina. Spongy layers up to 15 cells deep. *Air spaces*: large, substomatal cylinders perpendicular to surface; 30–90% space in spongy layer; or air cavities irregular in some species. Paradermally, spongy tissue with one layer of unarmed cells over abaxial epidermis, then small cells or short-armed cells surrounding large air cavities extending from stomata to palisade cells; 3–5 spongy cells per uniseriate partition. Large cavities in midrib separated by uniseriate partitions of ground tissue, partitions 3–4 cells long between junctions. *Collenchyma*: 4–5 discrete subepidermal layers of small cells on abaxial side of midrib, often extending to vascular bundles.

Vascular bundles. One to several large bundles in the midrib, often at corners of a net-like aerenchyma; well delimited, with 1–5 large metaxylem cells, next to a small, round or elliptic phloem strand. *Sclerenchyma*: fibers, usually as a phloem cap 1–3 layers deep, and less commonly as a xylem cap. Some laminar bundles ensheathed with fibers. Fibers having up to 5 discrete wall layers. Xylem cells often ringed with a single layer of small parenchyma cells. *Secretory ducts*: occasional in midlamina or midrib with 1–2 layers of epithelium. *Laticifers*: lateral to vascular bundles, 2–3 per bundle, outside fibers, often with short processes protruding between adjacent mesophyll cells; containing dark amorphous contents. *Starch*: abundant in midrib ground tissue, not seen in lamina. *Crystals*: raphides common or uncommon in single packets in short or elongate cells, ends protruding across partitions into both adjacent air spaces, or in large rounded cells of upper or lower mesophyll. Raphide packets occasionally surrounded by dark sheaths within the cell (in *P. crassispathum* crystal cells elongated parallel with vascular bundles). Druses rare or common, often coarse and sharp-pointed, in rounded cells in palisade and spongy tissue partitions. Crystal sand absent or common in most mesophyll cells.

Petiole Cross Section. Cuticle smooth and thin. Epidermis of small cells, level or rounded on surface and inner walls rounded to angular. Hypodermis of 2–4 layers. Collenchyma beneath hypodermis as a continuous band of 4–8 layers of angularly thickened, longitudinally elongated cells (8–10:1). *Chlorenchyma*: up to 5 rows of cells inside collenchyma, and in addition, in *P. jodavisianum*, as perpendicular partitions dividing the collenchyma band, and reaching subepidermal layers. Ground tissue of various sizes of parenchyma cells among numerous small to medium-sized air cavities separated by uniseriate partitions of up to 3 cells long. Cells often longitudinally elongated (3–6:1 l/w). Vascular bundles numerous and scattered, mostly oriented with phloem facing perimeter. Bundles are parallel in longitudinal section with some higher order angular connections. Xylem of 1–3 protoxylem cells per bundle, with spiral to annular thickenings, and occasionally one metaxylem element. Phloem of sieve cells and companion cells forming organized grid. In longitudinal section, sieve elements with horizontal to 45° oblique end walls. *Sclerenchyma*: fibers forming phloem cap, 2–4 cells deep, usually not fully surrounding phloem laterally. In some species, fiber caps surrounding xylem and phloem or ensheathing entire bundle.

Secretory ducts surrounded by epithelium and 1–2 rows of additional small cells, very common in

collenchyma and common in ground tissue. *Laticifers*: 1–3, found laterally on one or both flanks of vascular bundles; non-articulated. Starch common throughout ground tissue, rare in collenchyma. *Crystals*: narrow raphide cells occasional, oriented across aerenchyma partitions with ends pointing into air cavities, or cells randomly oriented. Druses present subepidermally and in cells bordering air cavities. Small groups of small prismatics common in ground tissue.

Stem Cross Section. 1–3 cm diam. Cuticle of medium thickness, smooth to rough-surfaced. Epidermis of very small cells, outer walls rounded. *Cork*: cells may be present subepidermally. *Hypodermis*: a subepidermal layer of large cells, over 1–2 layers of thick-walled fibers, followed by thin-walled periderm cells. *Collenchyma*: angularly-thickened cells, 3–10 layers deep, beneath periderm. Cortical ground tissue of loosely packed parenchyma. *Air cavities*: cell-sized or smaller in all ground tissue. *Central cylinder*: weakly delimited by a circle of vascular bundles, some of which tangentially fused in pairs or threes by phloem fibers and confluent phloem strands. Cortical bundles randomly scattered. Vascular bundles collateral and highly variable in form and orientation. Compound bundles numerous in central cylinder with irregular fiber strands in center of groups of 2–6 bundles. Small phloem strands outside fibers facing groups of 1–2 metaxylem elements on outer side. Simple collateral bundles may have a large wide strand of fibers surrounding phloem, a very small irregularly shaped strand of fibers, or no fibers. Fibers having up to 7 discrete wall layers visible.

Secretory ducts small and numerous in collenchyma and outer cortex, less common elsewhere. Duct cavities surrounded by two modified layers of small cells; contents of cavities testing positively for lipids. *Laticifers*: absent or present as 1–3 cells lateral to many vascular bundles, occasional in phloem. *Crystals*: raphides as single packets in elongate cells, most common in central cylinder. Druses of all sizes common in small cells in cortex.

Vascular anatomy. The configuration of shoot vasculature of *Philodendron* has been extensively studied by French and Tomlinson (1980, 1981, 1984). They reported the genus to be one of the most diverse in the family from an anatomical point of view. The axis of the vascular system of *Philodendron* is continuous throughout the stem because the renewal shoots develop precociously and because the morphologically terminal parts of the stem soon become branches (French & Tomlinson, 1984). All species of *Philodendron* examined by French and Tomlinson have an "independent cortical vascular system of traces that pass from the leaf into the cortex, but without entering the central cylinder." Generally the cortex is wide with 3–5 or more indistinct series of bundles. Cortical bundles are collateral, typically with a fibrous sheath next to the phloem. Major leaf traces enter the cortex at an acute angle and promptly enter the central cylinder, while smaller traces enter the cortex at a less acute angle and may enter the central cylinder well below where they entered the cortex. No endodermis was observed by French and Tomlinson for any of the species.

Philodendron subg. *Philodendron* has secretory resin canals occurring in the cortex. These consist of a schizogenous space lined with 2–3 layers of epithelial cells and contain a Sudan IV-staining resin (French & Tomlinson, 1984). The central cylinder is separated from the cortex by an arrangement of vascular bundles into which the leaf traces merge. Bud traces are equal on both sides and form an arc near the periphery of the central cylinder before joining with the axial bundles.

In their survey of 3-dimensional arrangement of vascular bundles, leaf traces and axial bundles were distinct, with the leaf traces consistently collateral with protoxylem and usually with a prominent sheath of sclerenchyma next to the phloem. The axial bundles were divided roughly into five groups, four of which pertain to *P.* subg. *Philodendron.*

In the *P. hederaceum* pattern (French & Tomlinson pattern 1) there are simple collateral bundles with some bipolar bundles in the central cylinder of the internodes with thin-walled and non-lignified ground tissue.

Another relatively rare pattern involving *P.* sect. *Baursia* (but not a Central American representative of the section) and *P. jacquinii* (pattern 3 of French & Tomlinson) has compound bundles throughout the central cylinder with individual compound bundles consisting of strands of xylem and phloem separated from each other by sclerenchyma "in the form of a partial or complete sheath" (French & Tomlinson, 1984). In *P. jacquinii* leaf traces enter the central cylinder but make a variety of configurations, sometimes including pairing before joining the compound bundles. Compound bundles do not make a particularly straight course, sometimes bundling and pairing within and between compound bundles.

A pattern of vascular bundle traces exhibited by *P. fragrantissimum* and *P. roseospathum* (French & Tomlinson pattern 4) is similar to pattern 3 except that "the pattern of the vascular components with

compound bundles is less clear because components are not separated by sclerenchyma" (French & Tomlinson, 1984). The sclerenchyma occupies the central core but does not isolate individual bundle components.

The pattern for *P. mexicanum* and *P. sagittifolium* (French & Tomlinson pattern 5), described as the most common in the genus, has axial bundles strictly amphivasal with a central core of phloem and a peripheral region of xylem. The tracheary elements may form a more or less continuous cylinder or may be arranged in clusters around the phloem. Leaf traces penetrate the central bundle and fuse with the central cylinder, while the sclerenchyma sheath of the trace migrates to the center of the axial bundle.

Habit and growth patterns. In terms of growth habit *Philodendron* is clearly one of the most variable genera in the Araceae (Blanc, 1977a, 1977b, 1978, 1980; French & Tomlinson, 1981). The habit ranges from terrestrial to epiphytic or hemiepiphytic (primary or secondary). Secondary hemiepiphytes may be vines or appressed-climbers.

Relatively few *Philodendron* species are terrestrial, although a few are consistently terrestrial. These include *P. glanduliferum, P. grandipes, P. malesevichiae,* and perhaps *P. hammelii* (known only from a single collection). The stem of *P. glanduliferum* (Fig. 198) is usually repent. Other species are mostly terrestrial, but sometimes hemiepiphytic: e.g., *P. basii, P. roseospathum* var. *roseospathum,* and *P. warszewiczii. Philodendron knappiae* is about equally terrestrial or hemiepiphytic. Label data regarding habit on herbarium collections are often suspect, with many herbarium labels using the term "epiphyte" when in fact the collections were probably rooted in the soil and were therefore technically hemiepiphytic. In addition, although many species have collections reporting them to be terrestrial, the majority were probably found on the ground as a result of accidentally falling from trees. Many collections are naturally made in virgin forest areas where man-made disturbances such as road building give access to the forest. In such areas, and especially in the regrowth along road cuts, aroids are very common. Many *Philodendron* species, e.g., *P. lentii* (Fig. 261) and *P. squamicaule* (Fig. 382), persist in excellent condition on steep roadbanks because the steep clay slopes allow adequate drainage for the plants to survive. Still, these are somewhat unusual situations. On the other hand, stream banks often provide similar habitats.

Many members of *P.* subg. *Philodendron* are hemiepiphytic, meaning that they are growing on trees as appressed climbers or as vines, while being rooted in the soil. There are two types of hemiepiphytes (Putz & Holbrook, 1986). Primary hemiepiphytes begin their lives when seeds germinate on the host tree, in the same way as true epiphytes, then go on to develop slowly until they reach sufficient age and size to begin developing long aerial roots that may eventually reach the ground. This growth strategy enables the species to quickly attain a height where light is adequate but nutrients are more difficult to obtain. Not surprisingly, one of the most successful species with this life form is *P. megalophyllum* Schott, which often lives on ant nests from which it obtains extra nutrients. No Central American species are known to live exclusively with associated ants, although occasional ant nests occur among the cluster of roots of many species. The roots hold the otherwise fragile ant nest to prevent it from being washed away in the rain. Examples of this type of hemiepiphyte are *P. goeldii* G. Barroso, *P. solimoesense* A. C. Sm., *P. megalophyllum* (all from South America), and *P. radiatum* (Fig. 1), the only species known with this growth form in Central America.

Secondary hemiepiphytes (Putz & Holbrook, 1986) start their lives on the ground or on tree trunks near the ground (where they may send roots to the ground) and climb trees where they become adults and may lose their connection with the ground. Most *Philodendron* sect. *Philodendron* are members of this group.

As is the case with most Araceae, adult plants of *P.* subg. *Philodendron* have homeophyllous monopodial growth[11] (monophyllous sympodial of Ritterbusch, 1971) with each article bearing a cataphyll and a leaf. When the plant is mature, each article is terminated by an inflorescence (Ray, 1986, 1987b) or its aborted remains (Engler, 1877; Ritterbusch, 1971). The branching pattern for *P.* subg. *Philodendron* has the prophyll following each internode suppressed, with a single foliage leaf followed by the inflorescences and with the internode subtending the prophyll of the elongation shoot being suppressed. Growth patterns for *P.* subg. *Philodendron* were diagrammed schematically by Engler

[11] "In monopodial growth, flowering occurs on axillary short shoots and does not interrupt the formation of the main shoot by a single apex. In monophyllous sympodial growth, after the shoot terminates in an inflorescence (which often aborts at the primordial stage), each continuation shoot will produce only a single foliage leaf before terminating in another inflorescence, and being replaced by another continuation shoot with one foliage leaf" (Ray, 1987b).

(1877) and Ray (1988) and discussed in detail by French and Tomlinson (1981). In contrast to adult plants of *P.* subg. *Philodendron*, the juvenile growth phase (with a few exceptions) has monopodial (actually anisophyllous sympodial) growth with an article bearing an indeterminate number of foliage leaves before terminating in the first (likely aborted) inflorescence, marking the transition into homeophyllous sympodial growth where each article has a fixed number of leaves and is terminated by an inflorescence or its aborted remains. This transition does not mean that stem has reached maturity. It has only made a transition from monopodial (actually anisophyllous sympodial) growth to homeophyllous sympodial growth. At this point, the plant is probably still not mature, and while every article will end in an infloresence, these will all be aborted. Later, after further thickening of the stem, the shoot will become mature, and this will be indicated by the fact that the inflorescences do not always abort (T. Ray, pers. comm.).

In contrast to *P.* subg. *Philodendron*, *P.* subg. *Pteromischum* has monopodial growth only up until the time of flowering when it is followed by anisophyllous sympodial growth, wherein the stem articles bear a variable number of leaves before producing another inflorescence. Each new branch forms from a bud in the "axil of the penultimate leaf of the previous unit" (French & Tomlinson, 1981). Both *P.* subg. *Pteromischum* and *P.* subg. *Philodendron* have development of the stem beyond each terminal inflorescence. Thus although *P.* subg. *Philodendron* appears to have an unbranched stem with an inflorescence in each leaf axil it is really producing a new branch after producing each leaf. Close examination will show that a bud for the renewal shoot occurs on each article just below the point of overlap of the sheath edges of the cataphyll (prophyll of Ray, 1987a). It is from this point that the new branch will form. There is also a second, supernumerary bud which lies below (proximal to) the bud for the renewal shoot. This acts as a reserve meristem, lying dormant unless the stem is severed just distally to it (French & Tomlinson, 1984).

Unlike *P.* subg. *Philodendron*, *P.* subg. *Pteromischum* typically does not branch after the production of each new leaf and therefore lacks comparable branch buds. The inflorescences are never produced terminally on determinate lateral branches (Grayum, 1996).

Internode length and width are altered markedly as the plant climbs, with the internodes getting ever shorter and thicker. Ray (1986) has shown a direct correlation between the length and width of an article (one segment of the stem) demonstrating that the length-width ratio is fixed and varies according to a set pattern. Ray (1987b) categorized four different types of stem segments based on where the leaf was attached to the stem. In *P.* subg. *Philodendron* all species had the petiole attached to the lower end of the stem segments, and these are referred to as "hypophyllous segments." Most species of *P.* subg. *Pteromischum* have "hyperphyllous segments" where the petiole is attached to the upper end of the stem segment. "Ambiphyllous segments," where the stem segment is so short that the petiole is attached across the entire segment, is also known in *P.* subg. *Pteromischum* and is also the most common type elsewhere in the family. The fourth type of sympodial stem segment, referred to as "peraphyllous segments" and presently known in the family only in *P.* subg. *Pteromischum*, has the stem segments elongated and extended below the point of attachment of the cataphyll.

Most members of *P.* subg. *Philodendron* have leaves that turn from juvenile to adult gradually as the plant climbs so that there is no abrupt transition to adult foliage.

Although not as pronounced as in *Monstera* or *Syngonium*, leaf dimorphy is present in some species of *Philodendron*. For example, in *P. hederaceum* var. *hederaceum* juvenile leaves have short petioles tightly appressed to the tree, more or less like the "shingle" leaves of *Monstera*. They are also dark blackish green and velvety above and often somewhat purplish violet beneath. The adult plants have spreading leaves with longer petioles and smooth, semiglossy blades. The velvety blades seem to be associated only with the earliest growth. Once the plant grows up high enough on the tree the leaves become smooth and semiglossy. Further growth, even when it represents a reversion to smaller-leaved forms, results in the same smooth, semiglossy texture as that of the adult.

Philodendron hederaceum and other scandent species tend to climb high up the trunk of the tree then spread into the canopy and finally often hang down from branches before they flower. *Philodendron jacquinii* often has a similar habit. Some scandent species, such as *P. brevispathum* and *P. sulcicaule*, typically sprawl over lower vegetation rather than high in the canopy.

The amount of internode elongation varies immensely in some vining species, such as *P. immixtum*, *P. hederaceum*, and *P. sulcicaule*, with internodes 10–20 cm long (even longer on plants that are juvenile or have reverted to a "searching mode" as the result of dislodgement from the tree). Usually internode length varies considerably depending on the light and nutrients available for growth. Even

fully adult plants with very short internodes can be induced to produce longer internodes in cases where the plant is accidentally displaced from its growing situation or if it becomes heavily shaded.

Some species have evolved the ability to produce flagellate branches in an attempt to reposition themselves. These have long slender internodes and reduced leaves. At first the flagelliform growth spreads laterally, but if no other growth support is in the immediate vicinity the branch inclines toward the ground where it may creep across the surface and ascend another tree. Blanc (1980) referred to these as "flagelles" or "stolons." Ray (1987b) indicated that these flagellate branches are usually developed when a plant overgrows its support or is accidentally dislodged, but in some species, e.g., *P. fragrantissimum*, the flagellate branches may develop from a normally growing plant (Croat, 1978). *Philodendron linnaei* Kunth, a South American species, has developed this method of locomotion to an extreme. That species produces a series of rosulate clusters of leaves all interconnected by more slender flagellate stems, which ascend the tree trunk. After a period of rapid growth resulting in long, narrow internodes with the leaves reduced to small scales, the plant produces a series of short thick internodes, each of which is associated with an increasingly larger leaf, and leaves arranged in a tight rosette (Ray, 1987b). Ray (pers. comm.) reports that "with only a few exceptions, flagellar shoots do not occur in species with homeophyllous growth. Flagellar shoots are almost universal among climbing species with anisophyllous or intermittent homeophyllous growth, but almost totally lacking among climbing species with homeophyllous growth."

Stems. Stems vary considerably in length depending on the nature of growth. Vines, such as *P. hederaceum*, may produce stems well over 30 m long, whereas the more slow-growing appressed climbing hemiepiphytes rarely have stems more than about 2 m long. The youngest part of the stem bears most of the leaves and has the newest root growth including the most active feeder roots. Older portions of the stem have thick, strong roots usually tightly fastened to the tree, anchoring it in place. Some roots all along the stem extend downward along the stem and may lead all the way to the ground. The older portion of the stem is often devoid of any leaves and usually lacks even cataphyll fibers. The bare stem clearly shows the petiolar and cataphyll scars (Figs. 9–12). See discussion below. Inspection usually shows that the older portions of the stem have been at some time attacked by root borers so there may be surface damage or more likely active root borers in the center of the stem. Eventually the lower part of the stem rots away as the stem climbs higher on the side of the tree.

Stems of *Philodendron* are typically unbranched, but may be branched naturally, as in many species of *P.* subg. *Pteromischum*, or through injury. Commonly internodes become increasingly shorter and thicker toward the apex of the stem on appressed-climbing plants, but some species, e.g., *P. fragrantissimum*, may from time to time begin to produce long slender internodes to enable the plant to enter a colonizing mode (see above section on "Habit and Growth Patterns").

Mayo (1991) described differences in the branching pattern of *P.* subg. *Philodendron* and *P.* subg. *Meconostigma*. While most *P.* subg. *Meconostigma* have very short internodes, some species, e.g., *P. leal-costae* Mayo & Barroso and *P. corcovadense* Kunth, have elongated internodes. In these species the elongated internode of each article is the one between the cataphyll (prophyll of Ray, 1987a) and the succeeding foliage leaf, while the internode preceding the cataphyll is abbreviated. In *P.* subg. *Philodendron* the elongated internode is the hypopodial internode (which precedes the cataphyll), while the internode between the cataphyll and the foliage leaf is the abbreviated one.

Stems of *Philodendron* are typically rich in taxonomic characters, and together with their associated cataphylls, yield some of the best key characters for identification. Normally these stem characteristics are useful only at the specific level, but Grayum (1996) has found the dried stem color to be useful in separating the two sections of *P.* subg. *Pteromischum*. Unlike most *Anthurium* species, which have internodes so short that the epidermal features are for the most part obscure or very uniform, *Philodendron* has features important both before and after drying. The internodes of most appressed-climbing hemiepiphytes are actually broader than long at maturity (Figs. 10, 394, 443), but some species, such as *P. advena* (Fig. 38) and *P. straminicaule* (Fig. 392), have internodes typically longer than broad (though short enough that the plants are not considered scandent). Only nine species in Central America have internodes longer than 25 cm on adult or preadult plants. Alternatively, many species have short internodes, with 33 Central American species having internodes to only 5 cm long or less.

Internode width is somewhat less variable, ranging from less than 3 mm diam. in *P. chirripoense* to 10 cm diam. in *P. gigas*. Only nine additional species (*P. chiriquense, P. copense, P. dressleri, P. fer-*

rugineum, *P. fortunense*, *P. grayumii*, *P. pterotum*, *P. schottianum*, and *P. warszewiczii*) have stems that attain diameters greater than 7 cm. Most species have relatively narrow internodes, with 44 species having internodes of no more than 3 cm diam., and 16 species with internodes of less than 1.5 cm diam.

Fresh stems often have characteristic surface features. Surfaces are frequently speckled with a lighter or darker pattern of green. The surface may also be short-lineate (Fig. 2) or may present a combination of short lines and speckles (Fig. 3). At other times the surface may be weakly to prominently striate as in *P. anisotomum*, *P. hederaceum*, and *P. wilburii*. The stems may be glaucous as sometimes in *P. dodsonii*, *P. fortunense*, *P. immixtum*, *P. ligulatum*, *P. mexicanum*, and *P. wendlandii*. Frequently the internodes are coarsely short-costate (Fig. 2) near the apex of the internode, as in *P. chiriquense*, *P. grandipes*, and *P. schottianum*. These apparently represent areas at which roots will emerge later.

Stems are commonly smooth but may be minutely wrinkled, as in *P. verrucosum*, or sparsely warty, as in *P. brunneicaule*, or setose, as in *P. jacquinii*, or with often branched, trichome-like scales (Fig. 5), as in *P. brevispathum*. Other species with scaly stems are: *P. hammelii*, *P. malesevichiae*, *P. squamicaule*, *P. squamipetiolatum*, and *P. verrucosum*. Even stems of species with smooth epidermis are often weakly fissured in fresh condition (Fig. 2).

Coloration of fresh stems may also be characteristic; typically, they are medium to dark green when fresh, turning gray-green to brownish, yellow-brown or reddish brown in age. Often several transitional stages are involved, e.g., medium green to gray-green, to yellowish green and finally yellowish or reddish brown. This final stem color is often the same as the color of the stem of artificially dried herbarium collections, but at other times the dried stem color of the herbarium collection is not the same. Thus it may be important to note the color of the fresh stem before drying takes place. Natural aging of the stems often causes a scurfy condition, which results from numerous close cracks (Figs. 4, 5). Sometimes these minute fissures are restricted to a specific point of stress yet not visible elsewhere (Fig. 5).

Another important feature is the extent to which the stem wrinkles or cracks or is otherwise distorted by the drying process. The results of the drying process are usually quite consistent from collection to collection, such that the dried stem and the features it exhibits provide useful recognition characteristics.

Stems commonly dry with irregular (or sometimes regular) ribs and intervening sulcae, reflecting shrinkage of the relatively indurate outer surface of the stem compared to the rather soft, somewhat aerenchymatous stem interior. In some cases the regularity and severity of this ribbing provide especially useful characteristics, e.g., in *P. sulcicaule* the stems of which become prominently ribbed in the course of normal development, and in *P. verapazense* where the stems become regularly and conspicuously ribbed on herbarium collections.

In addition to frequently present longitudinal ribs, in e.g., *P. findens*, *P. fortunense*, and *P. heleniae*, stems may be transversely fissured or checked with small to large fissures. These may be quite regular or irregular in severity or spacing. While sometimes characteristic, these transverse stem fissures tend to be somewhat less consistent than the longitudinal fissures. However, for some species such as *P. edenudatum*, *P. ferrugineum*, *P. findens*, *P. fortunense*, *P. ligulatum*, *P. malesevichiae*, *P. mexicanum*, and *P. wendlandii* (among others), the stems are frequently transversely fissured. Such stems are particularly noteworthy in an undescribed South American species, i.e., *Croat 62785* from the Pacific coast of Colombia.

Another feature exhibited by some dried stems is an exfoliating epidermis, present in *P. angustilobum*, *P. cotonense*, *P. dodsonii*, *P. hederaceum*, *P. schottianum*, *P. smithii*, *P. straminicaule*, *P. subincisum*, and *P. tripartitum*. In some cases the epidermis not only cracks but may begin to loosen and fall off or protrude away from the stem (Fig. 8), such as in *P. brevispathum*, *P. cotonense*, *P. dodsonii*, *P. ligulatum*, and *P. purpureoviride*. Occasionally this feature is exhibited on fresh stems as well. This is especially true if the stem is forced to bend by falling from its support, such as in *P. immixtum* and *P. sulcicaule*. The epidermis appears to be hard and brittle, while the underlying stem appears to be green and supple. In some cases the epidermis seems to be naturally shed and replaced by another epidermal layer on the fresh stem.

Petiolar scars. Although less conspicuous in general than in *Anthurium* or in *P.* subg. *Meconostigma*, the petiolar scars on the stems of *P.* subg. *Philodendron* are nonetheless clearly visible unless covered with persisting cataphylls. In contrast to *Anthurium* the petiolar scars of *P.* subg. *Philodendron* are generally much less indented but rather are more or less flush with the general contour of the stem surface. They may be moderately inconspicuous as in *P. rothschuhianum* (Fig. 9) or moderately conspicuous as in *P. davidsonii* (Fig. 10).

Philodendron petioles are typically much swollen at the base, so the scar is usually broader than the rest of the petiole itself. Petiole scars vary from (0.5–)1 to 4(–7.5) cm high and (0.7–)1 to 5(–7) cm diam., but they are rarely more than 3 cm high and 3.5 cm diam. The average height and width for the 32 species studied is 2 cm high and 2.4 cm diam. The peduncular scar is often quite conspicuous (Fig. 5) and deep. Of ecological significance is the fact that these deep holes left when the inflorescences fall off are the points of entry for phytophagous insects, especially stem borers, which infect the older and sometimes the younger portions of the stems.

Intravaginal squamulae (Dahlgren & Clifford, 1982), so prominent in *P.* subg. *Meconostigma*, are usually present but often inconspicuous in *P.* subg. *Philodendron* (Fig. 11). Mayo (1991) stressed this as evidence of differences in two contrasting patterns of stem elongation (see discussion under stem above). In *P.* subg. *Philodendron* the intravaginal squamulae (Fig. 11) are always immediately above the cataphyll (prophyll of Ray, 1987a), whereas in *P.* subg. *Meconostigma* the intravaginal squammulae are immediately below the cataphyll scars and often around the scar for the foliage leaf as well.

Roots. *Philodendron* roots have an anatomically distinct layer of exodermis beneath the epidermis, distinguished, among other things, by a long-cell/short-cell pattern (French, 1987a). "Thick-walled, pitted sclereids form a cylinder adjacent to the endodermis and similar sclereids also occur singly or in bands with suberized cork cells in the periderm of older roots" (French, 1987a). Like those of other members of tribe Philodendreae, *Philodendron* roots have a sclerotic hypodermis. French reported the scelerotic hypodermis to be distinctive because of its position next to the exodermis and its occurrence in the primary axis. Another distinctive anatomical feature of the roots of *Philodendron* is resin canals with sclerotic sheaths (French, 1987a).

All species of *Philodendron* produce adventitious roots at some or all nodes. The number of roots developed seems to have more to do with the environment than with the species involved. Plants that are appressed-climbing and in close contact with the substrate generally produce the largest number of adventitious roots. Roots may be of two types, which differ both morphologically and anatomically (Lierau, 1888; Porsch, 1911), either for anchoring the plant to the substrate or for feeding (van Tieghem, 1907; Went, 1893). The anchor roots (Fig. 54) tend to be more numerous and shorter, often with a dense layer of root hairs (they are sometimes restricted to the side of the root that contacts the substrate). They also have a proportionately much smaller central cylinder and more mechanical tissue to give them strength (Engler & Krause, 1908) than those of feeder roots. They arise principally at the nodes but may arise all along the internodes. Anchoring roots may spread from the nodes as in *P. auriculatum* (Fig. 12) or closely appressed to the surface of the tree on which they are growing as in *P. gigas* (Fig. 13). In contrast to the anchoring roots, the feeder roots (Fig. 14) tend to be much thicker and longer and usually extend toward the ground. This behavior is to be expected since Goebel and Sandt (1930) reported that feeder roots of aroids are negatively heliotropic and positively hydrotropic. Feeder roots have a much broader central cylinder and broader vessels and sieve tubes. Feeder roots arise only at the nodes (Grayum, 1990). Normally, the feeder roots are 2–4 times thicker than the anchor roots, and in *P. gigas* the feeder roots may be somewhat woody and up to 3.5 cm diam.

Some species, such as *P. auriculatum* (Fig. 12), have spine-like branch buds sparsely scattered along the length of the root, especially near the stem. Some hemiepiphytes, such as *P. solimoesense* A. C. Sm. in South America, have roots that may become markedly roughened with warty tubercles. In such cases the only portion of the root that has root hairs is the apex where the roots branch as they near the ground. It is unknown whether these roots are capable of absorbing atmospheric humidity, as is true for some *Anthurium* species, but certainly they must be able to take in the free water that runs down the root.

French (1987a) reported that in *P.* subg. *Philodendron* a sclerotic hypodermis is entirely absent in subterranean roots but present in the aerial roots. *Philodendron* subg. *Philodendron* has elongated, infrequently anastomosing resin canals that extend lengthwise through the root cortex (French, 1987c). They are lined with a layer of epithelial cells that consist of thin-walled, unlignified cells (parenchyma). In *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* the epithelium is surrounded by a sheath with lignified cell walls. In contrast, *P.* subg. *Meconostigma* has resin canal sheaths that lack a sclerenchyma and instead have 2–5 layers of (unlignified) collenchymatous cells, which are easily distinguished from the ground tissue (French, 1987c).

While seldom used taxonomically, roots are variable to some extent from species to species. Fresh root coloration (ranging from whitish to green to brownish), length, diameter, and surface texture

Table 2. Persistent condition of cataphylls by section.

Section	Deciduous		Persisting					
	Total	% of sect.	Intact	Semi-intact	As fibers	Total	% of sect.	Section total
Calostigma	34	69%	6	6	3	15	31%	49
Macrogynium	1	100%	0	0	0	0	0%	1
Philodendron	10	24%	0	18	14	32	76%	42
Polytomium	3	100%	0	0	0	0	0%	3
Tritomophyllum	7	88%	0	1	0	1	13%	8
Total	55	53%	6	25	17	48	47%	103

(smooth, coarse, or even warty), as well as the dried color and degree to which they are fissured or folded, are all features that may be recorded. These features have not been used extensively since the roots are generally removed from the stems before the herbarium specimens are prepared.

Cataphylls. In the taxonomy of *Philodendron* probably no morphological feature is more diagnostic than the cataphyll (sylleptic prophyll of Ray, 1987a). *Philodendron* exhibits considerable variation and remarkable consistency in cataphyll characters. Among the most valuable characters is whether the cataphylls are deciduous or persistent. This is the single feature that makes the preparation of keys to species of *Philodendron* easier than those for *Anthurium.* In *P.* subg. *Philodendron* 56 taxa have deciduous cataphylls, while 48 have persistent cataphylls. Of the latter, 6 have cataphylls that persist intact, 25 have cataphylls that persist semi-intact, and 17 have cataphylls that persist as fibers. While a few species have cataphylls tardily deciduous and others have persistent cataphylls that eventually fall off, relatively few species are difficult to place in one or the other category. See Table 2 for a breakdown of persistent condition of cataphylls by section.

Generally speaking cataphylls are deciduous in vines and persistent on appressed-climbing plants, but there are exceptions in both groups. Cataphylls are bract-like modified leaves which function in the protection of newly emerging leaves. For vines, the cataphyll becomes functionless once the leaf has emerged and generally is promptly deciduous. Typically it recurls away from the stem on vines and eventually becomes loosened from the base and falls free, such as on *P. purpureoviride* (Fig. 320). Alternatively, on epiphytes or appressed-climbing hemiepiphytes with short internodes the cataphylls cannot easily fall free (Figs. 15, 115, 312). Although they may fall free from the stem and invariably promptly dry and usually become withered or weather into fibers, they are often prevented from falling by the tight cluster of petioles generally found on plants with short internodes. They do regularly fall free on some species with short internodes, such as *P. warszewiczii* (Fig. 443) or *P. dressleri* (Fig. 160), but typically cataphylls persist on species with short internodes (Fig. 302, *P. pirrense*; Fig. 358, *P. scalarinerve*). Cataphylls often persist in an organized mass around the apex of the stem (Fig. 382, *P. squamicaule*). They may persist intact in *P. grandipes* (Fig. 204), *P. jodavisianum* (Fig. 248), and *P. roseospathum* (Figs. 341, 343), or have a very thin, flaky epidermis that remains intact in large pieces as in *P. dodsonii, P. hebetatum,* or *P. strictum* (Fig. 398); more frequently they decompose at least partially to expose a network of fibers beneath the epidermis (Fig. 258, *P. lazorii*), and even more frequently the epidermis disappears altogether (Fig. 202, *P. glanduliferum*; Fig. 253, *P. jodavisianum*; Fig. 370. *P. schottianum*). Ecologically the mass of cataphyll fibers serves a useful purpose, namely to prevent desiccation of the stem apex and especially the young roots which emerge through the moist cataphyll mass. In some species the layered cluster of cataphylls forms a sodden mass (Fig. 370, *P. schottianum*; Fig. 63, *P. antonioanum*; Fig. 99, *P. chiriquense*), and in some cases the youngest cataphylls are protected by a gelatinous, mucilaginous fluid that fills the interstices of the cataphyll mass. Cataphylls are generally rigid and firm when fresh, which protects the young leaf from physical damage. Some are thick and fleshy with considerable amounts of liquid in their tissues. As these begin to decompose they may yield large amounts of watery or even gelatinous sap. This fluid may be important as a lubricant for the emerging leaf to prevent damage to the tender tissues or to prevent desiccation. Since epiphytes are often subject to harsh conditions, this is probably important to protect the growing point of the plant and the newly emergent leaves from

extremes in temperature and humidity. Although the cataphylls soon lose their moisture after they have opened, many persist semi-intact or as an organized network of fibers so they continue to add protection to the stem apex. Even after the cataphylls are reduced to a mass of fibers they retain moisture much as a pile of straw does after a rain.

A typical cataphyll is narrowly triangular, 2.3–4 times longer than wide, with the base as broad as the circumference of the stem. It may be more than 1 cm thick toward the base on larger species. Cataphyll size is somewhat proportional to leaf size on any species, ranging from (5–)10 to 50(–70) cm long and (1.5–)2.5 to 18(–31) cm wide. Since the cataphyll is affixed around the complete circumference of the stem and eventually becomes deciduous, it leaves a distinct scar on the stem. These cataphyll scars alternate with the petiolar scars and may be conspicuous (Fig. 10, *P. davidsonii* subsp. *davidsonii*) or inconspicuous (Fig. 9, *P. rothschuhianum*). Fresh cataphylls are usually green, though in some cases almost white, as in *P. wilburii*; bright red, or heavily tinged red on exposed parts, such as in *P. antonioanum*, *P. niqueanum*, and *P. tysonii*; or reddish as in *P. glandulíferum*, *P. grandipes*, and *P. pirrense*. Cataphylls are often variously ribbed. In cross section they are frequently sharply D-shaped in outline but may be subterete. When subterete they may be unribbed or bluntly 1- or 2-ribbed (Fig. 60, *P. annulatum*; Fig. 16, *P. warszewiczii*; Fig. 17, *P. schottianum*) or sharply 1-ribbed. Those cataphylls which are D-shaped are often bluntly to sharply raised along the edges of the flat side so that they appear bluntly to sharply 2-ribbed, as in *P. pseudauriculatum* (Fig. 313). The ribs may be moderately low and closely spaced as in *P. panamense* (Fig. 298). In some cases the ribs are slender and knife-edged and may be as much as 1 cm high, as in *P. auriculatum* (Fig. 72) and *P. annulatum* (Fig. 60).

Useful taxonomic characters are found in the manner in which the cataphylls weather and persist. Cataphylls may be quite distinctive in the degree to which they persist intact or weather to fibers. The coloration of the cataphyll fibers is also variable, with colors ranging from almost white to tan, various shades of brown or yellow to reddish or reddish brown. Cataphylls are often short-lineate in the same manner as the petioles (Fig. 16). Some species have the network of fibers highly organized, while in other species the fibers are very disheveled, such as in *P. tenue* or *P. panamense*. In most species the epidermis of the cataphyll promptly falls off, while in some species all or parts of the epidermis persist. In *P. schottianum* the distinctive yellowish epidermis of the cataphylls is one of the most characteristic features.

In time the lowermost cataphylls simply rot away, even for species with a large cataphyll mass, so that ultimately the oldest part of the stem is visible. By this time the stem is quite old and few visible features are worth noting.

For many species the entire cataphyll does not persist, but rather only the basal part remains. Despite the fact that the stem is not covered with a large cataphyll mass, the stem is not easily visible. In such species the cataphyll bases seem to persist longer than in those cases where the entire cataphyll eventually falls free after persisting for a time.

Leaves. Leaves of *P.* subg. *Philodendron*, like those of *P.* sect. *Meconostigma* and *P.* sect. *Pteromischum* (indeed, most Araceae), have supervolute vernation (Cullen, 1978). Like most other aroids, *Philodendron* leaves undergo heteroblastic development, a gradual change in morphology from juvenile to adult forms (Grayum, 1990). However, heteroblasty in *P.* subg. *Philodendron* is not so severe as in other Araceae, especially in subfamilies Lasioideae and Monsteroideae. Typically, the juvenile blades are not dramatically different from those of the adults; commonly they are of similar shape as the adult blades, typically ovate to oblong, and virtually always lack posterior lobes. In rare cases, such as with *P. hederaceum* var. *kirkbridei* (Fig. 223), the juvenile blades are velvety, a feature that is caused by the markedly convex or even somewhat cone-shaped epidermal cells. Ecologically, this lack of glossiness has the effect of allowing nearly all light that falls on the leaf to be absorbed. In all but a few species, notably *P. gigas*, the velvety juvenile leaves are transformed to glossy or semiglossy adult leaves.

In terms of adult blade shape *P.* subg. *Philodendron* is exceedingly diverse, encompassing more morphological variation than is exhibited in *P.* subg. *Meconostigma* or *P.* subg. *Pteromischum* and indeed all the variation exhibited in the much larger genus *Anthurium*. Leaves are typically clustered at the end of the stem, and rarely more than ten are present at a time. Older leaves are eventually deciduous, falling free along with the petiole. In some rare cases the blades fall free first, followed by the somewhat more persistent petioles. The resulting petiolar scar (discussed above under stem) may not be apparent initially on species with persistent cataphylls, but even in these cases they are typically apparent on the older stems. Still, they are never so conspicuous as the petiolar scars in *P.* subg. *Meconostigma*.

In his review of leaf morphology and function Ray (1987a) divided leaves into three main types: foliage leaves, reduced leaves (10–70% the size of the foliage leaves), and cataphylls (reduced to less than 10% of a foliage leaf). The first leaf on a vegetative axis he refers to as a prophyll (in *Philodendron* always a cataphyll). This structure is usually 2-ribbed and is in this regard similar to the bracts that subtend inflorescences. The latter are referred to as bracteoles by Ray (1987a).

The leaf immediately following the prophyll is a fully developed leaf, referred to as a mesophyll (metaphyll of Grayum, 1996). All three types of leaves mentioned above may be modified by the terms proleptic and sylleptic, depending on the type of growth involved. Sympodial growth has petioles borne on the side of the stem, whereas monopodial growth has conspicuously sheathed petioles that encircle the stem. Any leaf subtending an inflorescence or an aborted inflorescence primordium is termed a sympodial leaf (Ray, 1987a). In *P.* subg. *Philodendron* all adult leaves are of this type. Juvenile leaves of *P.* subg. *Philodendron*, on the other hand, are all monopodial leaves (Grayum, 1990).

Petioles. Petioles of *P.* subg. *Philodendron* are usually elongated, sheathed only at the base in adult foliage and rarely with a conspicuous geniculum. Most species have blades as long as or longer than the petioles, but 63 species have blades at least sometimes shorter than the petioles. Twenty-one species have petioles reported as being as long as the blades, while 93 taxa have blades at least sometimes longer than the petioles. Petioles range in length from 4 cm in *P. bakeri* to 137 cm in *P. gigas*. Twenty-two species have petioles always less than 30 cm long, 11 less than 20 cm long, and only 4 species, namely *P. bakeri*, *P. brewsterense*, *P. chirripoense*, and *P. ubigantupense*, have petioles less than 15 cm long. Four taxa, *P. copense*, *P. radiatum* var. *radiatum*, *P. chiriquense*, and *P. tenue*, have petioles more than 1 m long.

Petioles range from less than 5 mm diam. on fresh petioles of *P. brewsterense* to ca. 7.5 cm diam. on *P. wendlandii* and *P. radiatum*.

Usually the petioles are erect-spreading from the stem with the blades either extending initially in the same plane or, more frequently, somewhat pendent from the end of the petiole.

Petiole cross section is not so variable in shape as in *Anthurium*, but the variation is important taxonomically. All too often herbarium collections make no mention of this frequently critical diagnostic feature. Typically petioles are obtusely somewhat flattened or sometimes broadly and obtusely sulcate at the base (Fig. 212). In either event they typically become more terete toward the middle and then obtusely somewhat flattened toward the apex (Fig. 18). Frequently also the petiole has an obtuse medial rib toward the apex where it becomes somewhat flattened.

The majority of *Philodendron* species have terete or subterete petioles. Sometimes the petioles are C-shaped, that is, subterete, yet also sharply adaxially sulcate. Forty-six taxa are described as having petioles subterete in cross section. Some species have subterete petioles with the adaxial surface also narrowly and obtusely sulcate as in *P. cretosum* (Fig. 126), *P. jacquinii*, *P. roseospathum*, and sometimes in *P. sagittifolium*.

Twenty-one Central American species of *P.* subg. *Philodendron* are described as having petioles variously D-shaped in cross section. Examples of species with D-shaped petioles are: *P. copense*, *P. findens*, *P. fortunense*, *P. fragrantissimum* (Fig. 187), *P. grandipes*, *P. jodavisianum*, *P. knappiae*, *P. lentii* (Fig. 264), *P. ligulatum* var. *heraclioanum* (Figs. 275, 276), *P. thalassicum*, and *P. verapazense*. Petioles of *Philodendron advena*, *P. pterotum*, *P. immixtum*, and *P. ligulatum* var. *ovatum* are also sometimes sharply flattened adaxially. Considerable variation exists in petioles described as D-shaped in cross section. Several species have petioles broadly and sharply sulcate, e.g., *P. bakeri*, *P. davidsonii*, *P. heleniae*, *P. lentii* (Fig. 264), *P. ligulatum*, *P. jodavisianum*, and *P. scalarinerve*. Rarely the adaxial surface is sharply and broadly concave and with the petiole often much broader than thick, as in *P. wendlandii* (Fig. 453). In the latter, the lateral margins may be very acute and directed outward. D-shaped petioles generally have the lateral margins weakly to prominently raised with the marginal rib either acute or obtuse. Taxa with the petiole margins acute comprise: *P. davidsonii*, *P. ligulatum* var. *heraclioanum*, and *P. wendlandii*. They are sometimes also acute on *P. chiriquense*, *P. llanense*, and *P. warszewiczii*. Sometimes, as in *P. findens*, *P. fortunense*, and *P. pterotum*, the margins are prominently winged. The wing is erect-spreading and may be markedly undulate in the area of the geniculum as in *P. fortunense* (Fig. 183) and *P. findens* (Fig. 171). Sometimes the petioles of *P. ligulatum* var. *heraclioanum* also may be weakly winged (Figs. 275, 276). Even petioles not D-shaped often have a slightly thickened, slightly raised lateral margin on the adaxial surface. Examples include *P. annulatum*, *P. cretosum*, *P. microstictum*, *P. thalassicum*, and *P. wilburii*.

Sometimes in addition to the raised margins of the petioles, there may be a prominent medial rib,

such as in *P. jodavisianum* and occasionally *P. grandipes*, giving the petiole a three-ribbed appearance adaxially. More commonly the medial rib is broad and obtuse, such as in *P. angustilobum*, *P. annulatum*, *P. copense*, *P. crassispathum*, *P. ferrugineum*, *P. ligulatum*, *P. llanense*, *P. schottianum*, *P. smithii*, *P. tenue*, *P. thalassicum*, and *P. tripartitum*.

Rarely the petioles may be markedly flattened dorso-ventrally, as in *P. platypetiolatum*. In this case the petioles are much broader than thick with the lateral margins nearly acute.

A few species have petioles markedly thicker than broad and U-shaped in cross section. Examples include *P. roseospathum*, *P. jodavisianum*, and sometimes *P. davidsonii*. Petioles of the latter species are more commonly obtusely V-shaped in cross section.

Petioles of *P.* subg. *Philodendron* typically have very short sheaths when the inflorescence is aborted and much longer sheaths (to accommodate the emerging inflorescences) when subtending an inflorescence (Figs. 38, 67, 93, 150). Generally the sheath is markedly closed with one margin overlapping the other, making it inconspicuous (Figs. 83, 160). Occasionally the petiole sheath may be conspicuous, such as in *P. correae* (Fig. 119) and some members of *P.* subsect. *Glossophyllum*.

A geniculum is typically not apparent, but the genicular area serves the same purpose as it does in *Anthurium*. It is involved with inclining or twisting the plane of the blade, presumably optimizing exposure to sunlight. Usually the genicular area is somewhat firmer than the remainder of the petiole, and sometimes it is differently colored, but it is usually neither swollen nor as conspicuously distinct as in *Anthurium*. Typically the genicular area is the same shape as the remainder of the petiole, but sometimes the cross-sectional shape is different, being more frequently bluntly ribbed and often rather deeply cracked or scurfy around the circumference (perhaps owing to the bending in response to light). The geniculum, when apparent, is sometimes thicker than the remainder of the petiole as in *P. brunneicaule*, *P. ferrugineum*, *P. heleniae*, and *P. tenue*. It may be darker than the petiole as sometimes in *P. bakeri* or *P. glanduliferum*, or slightly paler as in *P. ferrugineum* or *P. scalarinerve*.

Most species of *Philodendron*, like Araceae in general, have glabrous petioles, but there are conspicuous exceptions. Several species have conspicuously scaly petioles: *P. hammelii*, *P. glanduliferum*, *P. malesevichiae* (Fig. 283), *P. squamipetiolatum* (Fig. 387), *P. squamicaule* (Fig. 382), and *P. verrucosum*. The type of scales is also variable. In some species, such as *P. malesevichiae*, *P. glanduliferum*, and *P. squamipetiolatum*, the scales are acicular and more or less terete. The scales of *P. glanduliferum* and *P. malesevichiae* are spreading, while those of *P. squamipetiolatum* are sometimes retrorse near the apex of the petiole. In addition, they are densely granular-scurfy on the surface. In *P. hammelii* the scales are short and broadened laterally, similar to fish scales, and less than three times longer than broad. In *P. verrucosum* and *P. squamicaule* the scales are of two distinct types. *Philodendron verrucosum* has short, broad, and often lacerate scales interspersed with long-acicular scales. *Philodendron squamicaule* has short, purplish, deltoid, broader than high (about 2 mm high) scales interspersed among acicular, greenish scales 3–5 mm long.

Petiolar scales are not uniformly distributed along the petioles. In *P. squamipetiolatum*, *P. squamicaule*, and *P. verrucosum* the scales are usually scattered throughout the petioles. In *P. malesevichiae* they are present in the upper ½ to ⅓ of the petioles, becoming increasingly denser toward the base. In *P. glanduliferum* they are similar but more closely aggregated toward the apex. In *P. hammelii* the scales are restricted to a small area near the apex. *Philodendron ornatum* in South America is the most extreme example of this reduction. In that species the scales are reduced to stubby protuberances restricted to the apex of the petiole.

Surface features of both fresh and dried petioles are often conspicuous and frequently diagnostic. Though usually solid green, petioles may be irregularly purplish-spotted as in *P. edenudatum* (Fig. 163) and *P. sagittifolium*. This purplish spotting may continue onto the lower midrib, a feature common to other types of markings that continue onto at least the proximal portions of the midrib. The surfaces of petioles may be minutely speckled but more commonly bear a light pattern of short dashes or streaks usually uniformly distributed throughout the petiole. They may be densely to sparsely marked with short dashes, which in turn may be either darker or lighter than the surface. I have referred to this feature in the descriptions as "short-lineate" or "lineate." Though the lineations are usually short, usually less than 3 mm long, they may sometimes be longer and sometimes are variable in length with both short and long lines interspersed (Fig. 19). Examples of species with short-lineate petioles include: *P. annulatum*, *P. auriculatum*, *P. copense*, *P. cotonense*, *P. edenudatum*, *P. fortunense*, *P. immixtum*, *P. ligulatum*, *P. pirrense*, *P. purulhense*, *P. smithii*, *P. subincisum*, *P. thalassicum*, *P. warszewiczii*, and *P. zhuanum*. The peti-

oles of *P. brunneicaule* are red short-lineate. The short lineations may be associated as well with much longer, continuous, and frequently weakly raised striations or ribs. Species with petioles described as short-lineate to striate include: *P. antonioanum, P. clewellii, P. gigas, P. glanduliferum,* and *P. panamense.* Still other species have more or less continuous striations throughout: e.g., *P. anisotomum, P. davidsonii, P. dressleri, P. findens, P. madronense, P. rothschuhianum, P. straminicaule, P. tenue,* and *P. warszewiczii.*

Fresh petioles of *P.* subsect. *Glossophyllum* usually have a distinct purplish (or rarely dark green) ring (Fig. 20) around the entire petiole just below its junction with the blade. The species that share this feature, mostly members of *P.* subsect. *Glossophyllum,* include *P. annulatum* (Fig. 59), *P. bakeri, P. correae,* and *P. ligulatum* (all three varieties; see Figs. 271, 275) with a purplish or purple-black ring, and *P. auriculatum* (Fig. 20), *P. immixtum, P. dolichophyllum, P. pseudauriculatum,* and *P. wendlandii* with a dark green ring at the apex of the petiole.

Other apparently unrelated species may likewise have purple rings around the apexes of the petioles. These include *P. brenesii, P. davidsonii, P. dressleri, P. ferrugineum, P. microstictum, P. smithii, P. warszewiczii,* and sometimes *P. grayumii.*

Petioles may produce a cluster of viscid droplets of a sweet, sugary solution on the abaxial surface at the apex of the youngest leaves. This has been observed on *P. davidsonii* subsp. *bocatoranum* (Fig. 19) and *P. megalophyllum* Schott, a common South American species. These droplets appear to have no function in pollination or in blade orientation, and I speculate that they act as a food source for ant guards, which serve to prevent the young blades from predation by phytophagous insects. This seems all the more likely because the droplets are associated with new leaves, which are typically very tender and thus most easily damaged.

Freshly cut petioles usually form resin droplets in the same manner as the stems, and may in time become completely covered with resin. Of rare occurrence are slender strands of latex on broken and partially severed petioles as on *P. malesevichiae* (Fig. 21).

Dried petioles yield another suite of characteristics generally unrelated to those exhibited on fresh plants.

The dried petiole is sometimes diagnostic and in some cases, such as *P. hebetatum* and *P. schottianum,* petioles have a dried epidermis that is so conspicuously yellow-brown as to be nearly unique. Though less conspicuous, the petioles of *P. schottianum* and *P. thalassicum* also dry quite yellowish brown.

Petiole firmness is variable in *P.* subg. *Philodendron,* but this character is difficult to quantify. Unfortunately Engler used this character as one of his major key characters to separate subsections of *P.* sect. *Cardiobelium, P.* subsect. *Macrobelium,* and *P.* subsect. *Glossophyllum* with very fleshy petioles from *P.* Gruppe *Oligocarpidium,* and *P.* Gruppe *Doratophyllum* (now *P.* subsect. *Bulaoana*) with firm petioles. This character is difficult to describe and petioles appear to range from quite firm to quite spongy without any major discontinuities. Most species have petioles firm to weakly spongy when squeezed, and generally they are quite flexible, capable of being bent to a great extent without breaking. However, spongy petioles, such as those in *P. ligulatum* which can be easily crushed by squeezing, are also more likely to be brittle.

Blades. Blade shape. Virtually the entire range of morphological variation in leaf shape in the genus as a whole is exhibited among the Central American species of *P.* subg. *Philodendron.* The only blade shapes of *Philodendron* not shown by Central American species are those seen on *P. goeldii* G. Barroso in *P.* subg. *Meconostigma,* which has blades reniform in outline and pedately compound, and members of *P.* sect. *Schizoplacium,* which have blades pinnately lobed with a few, prominently falcate divisions. While *P.* subg. *Pteromischum* has distinctive leaves (even discounting the winged petiole on adult plants, which is definitive), their overall shape and size is matched by some other species of *P.* subg. *Philodendron.* Blade shape in *P.* subg. *Philodendron* relates in some cases to sectional differences. For example, species with three-lobed blades are either members of *P.* sect. *Tritomophyllum* or *P.* subsect. *Bulaoana.* Pinnately lobed species are members of *P.* sect. *Polytomium.* Some sections, especially *P.* sect. *Philodendron* and *P.* sect. *Calostigma,* are highly variable in blade shape, with that of *P.* sect. *Philodendron* ranging from oblong to variously ovate to ovate-sagittate and that of *P.* sect. *Calostigma* ranging from oblong to subcordate, prominently cordate, cordate-sagittate, or even 3-lobed. *Philodendron* subsect. *Glossophyllum,* relatively common in Central America, has more or less oblong, frequently subcordate or cordulate blades. See also section on "Discussion of Subgeneric Classification" for additional details.

While lobed leaves in some Araceae, e.g., *Monstera,* are due to necrotic processes in which growth stops and tissue rots away (Madison, 1977), the

lobed leaves of *Philodendron* are due to differential growth of leaf tissue.

In Central America more species have ovate-cordate blades than any other shape. In all variations, 38 species have some sort of ovate-cordate leaf blade. Twenty-two species are described as having ovate-cordate blades, and 11 as broadly cordate. Species with ovate to ovate-triangular leaves are most abundant among *P.* subg. *Philodendron* in Central America. At least 55 species have leaf blades with well-developed posterior lobes, including cordate, sagittate, and hastate. Only 15 species have non-cordate blades prominently longer than wide. Eight species have lobed blades, six trilobed, and two pinnately lobed. Species with trilobed leaves are: *P. anisotomum, P. cotobrusense, P. madronense, P. rothschuhianum, P. tripartitum,* and *P. angustilobum.* Species with pinnately lobed leaves are: *P. radiatum* and *P. warszewiczii.*

Posterior lobes. *Philodendron* subg. *Philodendron* species vary greatly in the shape of posterior lobes: usually rounded for those species with cordate leaf bases, e.g., *P. glanduliferum* (Fig. 197) or *P. platypetiolatum* (Fig. 306), or cordulate[12] leaf bases, e.g., *P. auriculatum* (Fig. 69), *P. immixtum* (Fig. 236), and *P. pseudauriculatum* (Fig. 314); to more or less oblong to narrowly triangular and much longer than wide as in *P. verapazense* (Fig. 434), or sometimes in *P. sagittifolium* (Fig. 346) and *P. tenue* (Fig. 404). Even in species with well-developed posterior lobes the lobes may be about as long as broad, as in *P. purulhense* (Fig. 322), *P. tysonii* (Fig. 426), or *P. schottianum* (Fig. 365). Posterior lobes may be sagittate as in *P. brunneicaule* (Fig. 95), *P. hebetatum* (Fig. 218), or *P. gigas* (Fig. 194); to hastate as in *P. angustilobum* (Fig. 49), *P. anisotomum* (Fig. 55), and *P. mexicanum* (Fig. 287); or bluntly triangular as in *P. wilburii* var. *longipedunculatum* (Fig. 461).

Sinus shape. *Philodendron* species with posterior lobes have remarkable variation in the shape of the sinus: merely arcuate, in *P. microstictum* (Fig. 289); arcuate with decurrent petioles in *P. morii* (Fig. 292); V-shaped in *P. glanduliferum* (Fig. 200), *P. lentii* (Fig. 263), *P. squamipetiolatum* (Fig. 386), and *P. tenue* (Fig. 406); oblong in *P. dwyeri* (Fig. 155); spathulate in *P. basii* (Fig. 76), *P. hebetatum* (Fig. 218), *P. smithii* (Fig. 372), and *P. rothschuhianum* (Fig. 339); parabolic in *P. sulcicaule*; hippocrepiform in *P. hebetatum* (Fig. 225), *P. lazorii, P. panamense* (Fig. 297), and *P. squamicaule* (Fig. 374); sometimes closed on live plants as in *P. fortunense* (Fig. 182), *P. gigas* (Fig. 194), *P. pterotum* (Fig. 311), and *P. schottianum* (Fig. 366). In *P. fortunense* and *P. subincisum* (Fig. 401) the sinus may be closed even on pressed plants. The shape of the sinus varies greatly between live and flattened dried plants, since the shape of the sinus varies depending on the angle at which the posterior lobes are turned up in relation to the midrib. Many species have the posterior lobes turned upward at an angle to the midrib on live plants (see, e.g., Figs. 104, 130, 159, 186, 366, 374), causing the inner margins of the posterior lobes to become closer to each other and thus decreasing the apparent size of the sinus. For example, when the angle of the posterior lobes is extreme the posterior lobes might be closed, but when the same blade is flattened and dried the sinus might become spathulate or hippocrepiform. The description of the sinus as presented in this work for Central American *P.* subg. *Philodendron* is exclusively that of the flattened sinus unless otherwise stated.

The sinus shape may be intraspecifically variable as in *P. sousae,* for example, with the sinus ranging from spathulate (Fig. 379) to parabolic (Fig. 380). This is in part related to the age of the plant, with older plants bearing larger blades that have larger, more well developed posterior lobes.

Blade size. Blades of *P.* subg. *Philodendron* in Central America as elsewhere are highly variable in size, but relatively few have blades that are considered huge. Only 19 Central American species of *P.* subg. *Philodendron* have blades that exceed 75 cm long (although many others approach that size). Of these, only *P. gigas* has blades that regularly exceed 1 m in length, with the maximum recorded at 137 cm. The blades of *Philodendron ferrugineum* may rarely exceed 1 m in length. By the same token few species in Central America have small leaves. Only 37 species have blades less than 25 cm long on adult plants, and of these only 13 have blades less than 15 cm long. *Philodendron brewsterense,* with blades a maximum of 11 cm long, is the species with the smallest leaves, and *P. chirripoense,* with blades up to 11.6 cm long, has leaves about as small. The median leaf length for *Philodendron* in Central America is 57 cm.

The widest blades belong to *P. gigas* and *P. radiatum* (to 90 cm long), but *P. pterotum* (to 84 cm wide), *P. findens* (to 70 cm wide), *P. dodsonii* (to 66

[12] With miniature lobes held very near the petiole (see photos of *P. auriculatum*) as compared to subcordate, wherein the lobes, though short, are usually broadly rounded with each lobe encompassing about half the width of the entire blade.

cm), *P. schottianum* (to 64 cm), and *P. warszewiczii* (to 62 cm) also have quite broad blades.

While blade size of *Philodendron* is often not reliable for taxonomic separation and even blade shape is sometimes unreliable, the length-width ratio is, in general, more reliable as a taxonomic character. Blades range from being much broader than long, to more than eight times longer than broad (in *P. cretosum*), to broader than long. Blades are broader than long in a number of species, e.g., averaging only 0.62 times as long as broad in *P. anisotomum* and *P. bruneicaule* and 0.7 times as long as broad in *P. cotobrusense* and *P. grayumii*. The average blade length-width ratio for species with simple, unlobed leaves ranges from 1.6 to 2.5 times longer than wide. Exceptions include *P. cretosum* and *P. folsomii* (8.3 and 5.2 times, respectively).

Blade margins are typically entire on simple leaves, never toothed and only rarely sinuate, such as in *P. subincisum*. Species with weakly sinuate blades are: *P. basii*, *P. dwyeri*, and *P. jefense*. On the other hand, blade margins are frequently undulate to a certain extent, especially on larger blades. Species that have coarsely undulate leaves are: *P. annulatum*, *P. antonioanum*, *P. copense*, *P. ferrugineum*, *P. fortunense*, *P. grandipes*, *P. hebetatum*, *P. panamense*, and *P. sulcicaule*.

Blade margins are frequently hyaline and also often weakly revolute. Examples of species with hyaline blade margins are: *P. advena*, *P. crassispathum*, *P. davidsonii*, *P. ferrugineum*, *P. gigas*, *P. immixtum*, *P. hederaceum*, *P. smithii*, *P. squamicaule*, *P. straminicaule*, *P. subincisum*, and *P. wilburii* var. *longipedunculatum*.

The coloration of leaf blades is highly variable and largely dependent on the habitat, but some species, such as *P. roseospathum*, *P. scalarinerve*, and *P. tysonii*, have very dark green blades while others (e.g., *P. lazorii*) have lighter green blades. A few species, such as *P. chiriquense*, have purple coloration on young leaf blades but most lose this coloration in age. An exception is *P. verrucosum*, which has adult blades generally purplish on the lower surface. A few taxa such as *P. ligulatum* var. *heraclioanum* (Fig. 274) and *P. sagittifolium* have leaf blades purplish-spotted on the lower surface, especially when young. Coloration of lower blade surfaces is more often restricted to the major veins, which are frequently reddish (along with the young petiole) as, for example, in *P. antonioanum*.

Venation. Midribs. Leaf midribs of *P.* subg. *Philodendron* are more variable in cross-sectional shape than those of other aroid genera, such as *Stenospermation*, *Rhodospatha*, *Spathiphyllum*, and *Monstera*, yet not as taxonomically significant as in the related genus *Dieffenbachia*.

Midribs on the upper (adaxial) blade surface of *P.* subg. *Philodendron* are highly variable, being flattened or variously sunken or raised (sometimes even in the same species). Fifty-six species have adaxial midribs at least sometimes raised, 26 have upper midribs at least sometimes sunken (only *P. cretosum* has a deeply sunken midrib), and 54 have adaxial midribs sometimes flat. Only 12 taxa, *P. antonioanum*, *P. aromaticum*, *P. albisuccus*, *P. coloradense*, *P. dressleri*, *P. granulare*, *P. pirrense*, *P. purulhense*, *P. strictum*, *P. warszewiczii*, *P. wilburii* var. *longipedunculatum*, and *P. zhuanum*, are described as having strictly flattened adaxial midribs. Fifteen species are described as having only convex midribs, and 15 are described as having only sunken midribs. Only 2 species, *P. morii* and *P. niqueanum*, are described as having the adaxial midribs prominently raised.

The adaxial midrib is nearly always to some extent paler than the surface. In only 12 species are the midrib and the blade concolorous. An additional 8 species have midribs concolorous to slightly paler.

The lower (abaxial) midrib of *Philodendron* blades exhibits less variability. All species have adaxial midribs to some extent raised. A few species, e.g., *P. crassispathum*, have the abaxial midrib so broadly convex as to appear nearly flat, but most species have the midrib noticeably raised. The abaxial midrib is generally convex but often narrowly rounded, thicker than broad, and sometimes bluntly acute. Species with the abaxial midrib weakly raised are rare in *P.* subg. *Philodendron*. Only seven species have abaxial midribs at least sometimes described as broadly convex or weakly raised: *P. anisotomum*, *P. crassispathum*, *P. fortunense*, *P. microstictum*, *P. platypetiolatum*, *P. purpureoviride*, and *P. straminicaule*.

Many more species have abaxial midribs more prominently raised. In the largest category, 47 species have abaxial midribs more or less convex, i.e., more or less hemispherical in cross section. Thirty-six species have abaxial midribs described as thicker than broad, narrowly convex, narrowly rounded or bluntly acute at least part of the time. A number of these species have abaxial midribs so prominently raised as to be noticeably thicker than broad: *P. copense*, *P. cretosum*, *P. dolichophyllum*, *P. hebetatum*, *P. heleniae*, *P. jodavisianum*, *P. panamense*, and *P. roseospathum*. Taxa that have abaxial midribs sometimes thicker than broad are *P. scalarinerve* and *P. wilburii* var. *longipedunculatum*.

The most extreme type of raised adaxial midribs

is so raised as to appear to be a cylinder attached tangentially to the surface of the leaf. This type of midrib has been referred to as "round-raised." Examples of species with such midribs are *P. brunneicaule*, *P. dressleri*, *P. madronense*, *P. squamipetiolatum*, and *P. radiatum*. In cases where the midrib is round-raised, the primary lateral veins are also sometimes round-raised.

While the abaxial midrib is more likely than the adaxial midrib to be concolorous with the rest of the blade or darker than the remaining blade surface, 45 species still are reported as having the midrib paler than the surface. Twenty-four species have the abaxial midrib described as darker than the surface.

A number of species, including *P. edenudatum*, *P. grayumii*, *P. ligulatum* var. *ligulatum*, and *P. sagittifolium*, have one or both midribs maroon- or purplish-spotted.

Primary lateral veins. The primary lateral veins (referred to by some authors as "secondary veins") are those that branch off the midrib and extend to the margins usually without additional branching. This use of primary lateral vein is consistent with that of early aroid workers Engler, Krause, and Sodiro. Engler and later Krause referred to the primary lateral veins as "nervis primariis." Sodiro also referred to the primary lateral veins as "nervis lateralibus I."

On larger cordate blades there is frequent branching of the primary lateral veins in the lower part of the blade where primary lateral veins are widely spaced (Fig. 26) (see also Croat & Bunting, 1979). The presence of these veins, referred to here as "secondary veins," is not commonly indicated in this work, but in shape and aspect they are virtually the same as the primary lateral veins (Fig. 24).

Both surfaces of the blade typically have primary lateral veins similar to the associated midrib. Usually they are somewhat less prominently raised than the midrib. The primary lateral veins on the upper (adaxial) surface, while usually sunken, may be essentially flat with the surface. Sometimes they are raised but at the same time contained within a broad or narrow valley so that the veins appear to be sunken. Primary lateral veins may sometimes be "quilted" (Figs. 23, 200, 361), i.e., with the veins deeply sunken and with the intervening leaf tissue of the blade that lies between the primary lateral veins being broadly raised, making the surface appear like that of a plush quilt.

Primary lateral veins of *P.* subg. *Philodendron* are rarely either absent or so inconspicuous as to appear to be absent, such as in *P. brewsterense*, though they are sometimes not at all conspicuous, as in *P. microstictum* (Fig. 289) or *P. sulcicaule* (Fig. 403). The number of primary lateral veins varies from 2 pairs in *P. chirripoense* to 25 pairs in *P. madronense*. Most species have 3 to 6 pairs of primary lateral veins. These generally arise at an acute angle with the midrib and, after extending along or near the midrib, spread at an angle of generally 40–80° toward the margins, generally forming a broad arc in the process. The angle of primary lateral veins for all species may be as little as 5° to as much as 100°. When species of Central American *P.* subg. *Philodendron* are divided into a series of range categories based on the angle of their primary lateral veins, more species (eight) have primary lateral veins spreading at 50°–60° angle or at 60°–70° (also eight species) than any other group.

Basal veins. Primary lateral veins that contact the plexus at the base of the blade and the apex of the petiole are here referred to as "basal veins" (Fig. 22) (see also Croat & Bunting, 1979). While the uppermost 1 or 2 pairs usually extend upward and into the anterior lobe where they join the antemarginal vein, most extend into the posterior lobes. Generally, basal veins are best developed on plants that have posterior lobes and are not present, or at least are few in number, when the blade lacks posterior lobes. Basal veins, like the primary lateral veins, are typically paired, with usually an equal number on either side of the midrib.

Seventy-three species (75 taxa) of *P.* subg. *Philodendron* in Central America have basal veins. The number of pairs of basal veins ranges from 1 to 15, but only eight species (*P. angustilobum*, *P. copense* (to 15), *P. findens*, *P. grandipes*, *P. thalassicum*, *P. pirrense*, *P. squamicaule*, and *P. strictum*) have 10 or more pairs. Most species have 3–6 pairs of basal veins, though up to 16 species may have only 2 pairs of basal veins. Only three species, namely *P. lentii*, *P. mexicanum*, and *P. scalarinerve*, regularly may have a solitary pair of basal veins.

Posterior ribs. The basal veins are generally to some extent coalesced near their union with the petiole. The union or coalescence of basal veins is here referred to as the "posterior rib" (Figs. 22, 25) (see also Croat & Bunting, 1979). Sixty-three species (65 taxa) have the basal veins at least in part united and thus possess posterior ribs, while 34 species (38 taxa) have the basal veins free to the base (or lack basal veins all together) and thus lack posterior ribs. Both the number and nature of basal veins and the length of the posterior rib are good characters for distinguishing taxa. The basal veins

may be completely coalesced for a distance (Fig. 22) or loosely coalesced. The posterior rib may be prominently naked for a distance (Figs. 22, 169) or barely (Figs. 26, 211) or not at all naked (Figs. 161, 163, 287). The basal veins are free or nearly so in most species with rounded or cordulate leaf bases (Fig. 20). Such species are: *P. auriculatum*, *P. bakeri*, *P. correae*, *P. chirripoense*, *P. cretosum*, *P. dolichophyllum*, *P. granulare*, *P. immixtum*, *P. lentii*, *P. ligulatum*, *P. pseudauriculatum*, *P. roseospathum*, *P. scalarinerve*, *P. ubigantupense*, *P. utleyanum*, and *P. wendlandii*. Even species with short or poorly developed posterior lobes, such as *P. annulatum*, *P. clewellii*, *P. davidsonii*, *P. microstictum*, *P. niqueanum*, and *P. platypetiolatum* usually have the basal veins free to the base. On the other hand, species with well-developed posterior lobes usually have the basal veins coalesced to some degree. Posterior ribs range from less than 0.5 cm long (in *P. straminicaule*) and 1 cm long (in *P. angustilobum*, *P. basii*, and *P. alticola*) to more than 14 cm long in *P. gigas*.

Another important taxonomic character is the extent to which the posterior rib is naked along the sinus. In general, the longer the posterior rib the more likely it is to be naked at least to some extent along the sinus. However, *P. tenue* is exceptional in having a well-developed posterior rib and being not naked along the sinus. The degree to which the posterior rib is naked along the sinus varies from as little as 0.5 cm in *P. straminicaule* to 6 cm in *P. squamicaule*. Examples of species with prominently naked posterior ribs are: *P. albisuccus*, *P. alticola*, *P. aromaticum*, *P. basii*, *P. brunneicaule*, *P. copense*, *P. dodsonii*, *P. dressleri*, *P. findens*, *P. hebetatum*, *P. knappiae*, *P. panamense*, *P. purulhense*, *P. strictum*, *P. thalassicum*, and *P. verapazense*.

Lesser order veins. Between successive primary lateral veins there are possibilities for two additional orders of veins. Frequently present are intermediate primary lateral veins here called "interprimary veins" (Figs. 24, 26) (see also Croat & Bunting, 1979). These veins, while decidedly less conspicuous than the primary lateral veins, are nevertheless too prominent to be classified as the smallest-order veins. To qualify as an interprimary, the vein must extend continuously from the midrib to very near the margin without major branching. Generally there is no more than one pair of interprimary veins between alternate primary lateral veins. They are akin to the primary lateral veins in all aspects except for their reduced size. Like the primary lateral veins they may bear minor veins, which may form all along their margins.

The smallest-order veins are here referred to as "minor veins" (Fig. 24) and may be close, fine, and conspicuous as in *P. sulcicaule*, *P. tripartitum*, and *P. radiatum*, to thick, well-spaced, and inconspicuous in *P. gigas*, *P. granulare*, *P. grayumii*, and *P. ligulatum*. The minor veins are not all equally distinct and sometimes, as in *P. dominicalense*, the minor veins are alternately weakly visible and strongly visible.

The minor veins may arise from the midrib or from the primary lateral and interprimary veins, but in either case they form a generally close, uniform, and parallel array, which extends without interruption to near the margin of the blade. In most species the minor veins arise from both the midrib and the primary lateral veins, but some species have the minor veins arising from only the midrib. A total of 77 species (81 taxa) have the minor veins arising from both the midrib and the primary lateral veins (Fig. 26). In such cases the minor veins are not always equally arising from one of the two entities but may, as in the case of *P. brenesii*, *P. davidsonii* subsp. *davidsonii*, *P. ferrugineum*, and *P. tripartitum*, be more heavily arising from the midrib rather than the primary lateral veins. In *P. auriculatum*, *P. glanduliferum*, *P. lentii*, and *P. ligulatum* the minor veins arising from the primary lateral veins are many fewer than those arising from the midrib. In *P. heleniae* the primary lateral veins are only rarely arising from the midrib.

In another variation of this venation type, some species, while having minor veins arising from the midrib as well as both adjacent primary lateral veins, have considerably more veins arising from the distal primary lateral vein than from the proximal vein.

A total of 24 species have the minor veins arising from only the midrib, and in this case they course along the primary lateral veins but do not join with it. Many of the species that have the minor veins arising only from the midrib are species with oblong blades, such as: *P. bakeri*, *P. cretosum*, *P. dolichophyllum*, *P. granulare*, *P. heleniae*, *P. roseospathum*, *P. ubigantupense*, *P. utleyanum*, and *P. wendlandii*. However, this group also has blades ovate or nearly so as in *P. brewsterense*, *P. chirripoense*, *P. cotobrusense*, *P. crassispathum*, *P. folsomii*, *P. knappiae*, *P. microstictum*, *P. niqueanum*, *P. sulcicaule*, and *P. verapazense*. Interestingly, *P. anisotomum*, with deeply 3-lobed leaf blades, also has the minor veins arising from only the midrib, whereas *P. tripartitum*, a similar species with 3-lobed blades, has the minor veins arising from both the midrib and the primary lateral veins.

Philodendron dressleri, a species with deeply di-

vided leaves, has a more complex venation pattern. Although the minor veins arise from both the midrib and the primary lateral veins, they also arise from short secondary veins that regularly branch off the primary lateral veins. In addition, the minor veins that arise from the midrib are considerably fewer in number and weaker than in most species with this venation pattern. Generally, the confluent minor veins that arise from the primary lateral veins and make a broad sweep before continuing to the margin leave little area for the minor veins, which arise from the midrib. The latter tend to merge imperceptibly with those from the primary lateral veins. A similar pattern with weak midrib-borne minor veins is present with *P. basii.*

At or very near the margin both the primary lateral veins and the minor veins generally turn sharply toward the apex of the blade. The minor veins join with other minor veins and with the primary veins before finally merging into an inconspicuous and somewhat opaque marginal plexus. This narrow band is usually chlorophyllous and apparently veinless. Frequently the outer margin of this chlorophyllous band is a hyaline edge, which is colorless and typically revolute.

The minor veins are sometimes noticeably interconnected by inconspicuous to conspicuous veins, referred to here as "cross-veins" (Fig. 26). Generally the cross-veins are markedly perpendicular to consecutive minor veins where they are sufficiently prominent to be noticeable, but in some cases the cross-veins cross transversely from one minor vein to the next. While *P. scalarinerve* has cross-veins so prominent, even on fresh material, as to be easily visible, other species such as *P. chiriquense* and *P. copense* have cross-veins easily visible only when the blades are dry.

Secretory ducts and other secretory tissues are frequently present on Central American members of *P.* subg. *Philodendron.* The contents of the secretory ducts are either latex or tanniniferous compounds (Solereder & Meyer, 1928). No thorough survey has been made of the nature of the secretory canals in Central American species, so it is not always apparent whether these structures are resin canals or secretory ducts. Secretory canals (also referred to as secretory files) in *Philodendron* are always non-anastomosing and consist of a linear sequence of secretion cells, each separated from the next by cell walls (Solereder & Meyer, 1928). On fresh and dried leaves these can usually be recognized by being darker, usually blackened, and in being intermittent rather than continuous as is generally true of veins. While the distribution of secretory ducts in *Philodendron* may be more common than is apparent from surface examination, not all species exhibit the secretory ducts clearly. Thus the presence or absence of distinct secretory ducts can be useful taxonomically. They are distinctly visible on *P. alticola, P. cotonense, P. grayumii, P. heleniae,* and *P. zhuanum,* but obscurely visible on *P. antonioanum,* and *P. bakeri.* They are clearly visible on *P. schottianum,* somewhat visible on *P. llanense,* and obscure on *P. findens,* even though these three species have very similar leaf blades.

While perhaps no more reliable than blade shape, blade size, or other features, blade surfaces at a magnification of 10× or higher often reveal another suite of characters, which often yields another degree of confidence (or forewarns of misidentification) when making determinations. The surface between the minor veins is frequently marked by pale sub-surface granulations (perhaps indicating the presence of druse crystals), short, pale lineations, gland-like punctiform markings, reddish or brownish speckling, and also what might be referred to as "stitching," pale intermittent short lines appearing on the surface of the blade as though the blade was loosely sewn with a needle and thread. Though this phenomenon is much more common in *P.* subg. *Pteromischum,* it is also exhibited in *P.* subg. *Philodendron.*

Morphology of Reproductive Structures

Inflorescences

When a plant of *P.* subg. *Philodendron* flowers, the stem apex is terminated by an inflorescence (or frequently an aborted inflorescence primordium) (Ritterbusch, 1971; Blanc, 1977c; Madison, 1978) and new growth is from a bud in the axil of the penultimate leaf. This new growth pushes aside the newly developing leaf and the inflorescence that is developing in its axil (Ray, 1987a). When the inflorescences abort, the petiole sheath remains quite small and unexpanded, but when the inflorescences develop, the sheath may be much larger. *Philodendron* inflorescences are sympodial, with each sympodium consisting of 1–10 (to 11 in South America) inflorescences arising typically in what appears to be the leaf axil of usually one of the upper leaves (but almost never in the uppermost leaf axil). Often inflorescences emerge from the mass of cataphyll fibers, enabling the inflorescence to remain moist (Figs. 63, 115, 188, 371, 430). The individual inflorescences are subtended by and enclosed in a series of moderately coriaceous, whitish to pinkish, 2-ribbed structures (Fig. 195, *P. gigas,* Fig. 428, *P. tysonii*) called bracteoles (Ray, 1987a). These have elsewhere been referred to as prophylls (Usher,

1966; Jackson, 1971). At anthesis the bracteoles are typically deciduous, although sometimes they persist for a time simply because they are held so tightly by the developing infructescences.

Typically the inflorescences are borne in the erect or semi-erect position regardless of the position of the stem. Even when the inflorescence is borne on the end of a pendent stem, the stem usually curves upright so that the opening inflorescence is erect at anthesis (Fig. 273, *P. ligulatum* var. *ovatum*; Fig. 269, *P. ligulatum var. ligulatum*).

The number of inflorescences per axil is taxonomically significant. More species (38) have a solitary inflorescence per axil (or are believed to have a solitary inflorescence) than any other combination. Many others may be found with only a single inflorescence if they are seen in the early stages of flowering or if inflorescences have aborted owing to lack of pollination, but plants frequently have two or more inflorescences per axil later in the flowering season. Careful dissection of the leaf axil usually can provide evidence of the peduncular scar indicating a lost inflorescence. Taxa known to usually have only a single inflorescence per axil are: *P. albisuccus, P. anisotomum, P. aromaticum, P. bakeri, P. basii, P. breedlovei, P. brevispathum, P. brewsterense, P. brunneicaule, P. chirripoense, P. correae, P. cotonense* (rarely 2), *P. crassispathum, P. dressleri, P. dwyeri, P. edenudatum, P. folsomii, P. glanduliferum, P. granulare, P. hammelii, P. hederaceum, P. immixtum, P. jacquinii, P. jefense, P. knappiae, P. ligulatum* var. *heraclioanum, P. ligulatum* var. *ligulatum* (sometimes 2, rarely to 5), *P. ligulatum* var. *ovatum, P. madronense, P. mexicanum, P. microstictum, P. platypetiolatum* (rarely 2), *P. purpureoviride, P. purulhense, P. radiatum* var. *pseudoradiatum, P. squamipetiolatum, P. utleyanum, P. verapazense*, and *P. warszewiczii* (rarely to 3).

Most species with a single inflorescence per axil are either vines or appressed-climbing hemiepiphytes with internodes longer than broad.

The number of upper axils bearing inflorescences is also variable. Some species, e.g., *P. lentii*, rarely have more than one leaf axil bearing an inflorescence, while other species, e.g., *P. annulatum* and *P. fragrantissimum*, bear inflorescences in two or more of the closely spaced upper internodes, making it appear that the plants have a large number of inflorescences.

Species that regularly have up to four or more inflorescences per axil are: *P. copense* (to 6), *P. cotobrusense* (to 5), *P. clewellii* (to 6), *P. dodsonii* (2–5), *P. ferrugineum* (to 6), *P. fortunense, P. gigas* (to 7), *P. grayumii* (to 5), *P. heleniae* (to 10), *P. jodavisianum* (2–6), *P. panamense* (to 6), *P. pirrense, P. squamicaule* (to 5), *P. sousae, P. tenue, P. tysonii* (to 5), and *P. verrucosum.*

Species with five or more inflorescences per axil are rare, totaling only eleven. Only two species, *P. gigas* and *P. heleniae*, have up to seven inflorescences per axil.

PEDUNCLES

Typically the peduncle is terete but it may be somewhat flattened laterally, especially when there are clusters of inflorescences per axil. The peduncle is usually whitish or pale green at the base where it is often hidden by the leaf sheath. The remaining portion of the peduncle is usually dark to medium green with the surface often shortly pale-lineate like the petioles. The peduncle is often coarsely pale-ribbed near the apex, as in *P. copense, P. dodsonii*, and *P. findens.* Rarely is the peduncle pinkish red or reddish as in *P. malesevichiae, P. schottianum*, and *P. roseospathum* (or sometimes in *P. sulcicaule*) or tinged with red or purple as in *P. chiriquense, P. davidsonii* subsp. *bocatoranum, P. heleniae, P. grandipes, P. purpureoviride*, and *P. verrucosum.*

Most peduncles, like other parts of the average *Philodendron*, are glabrous, but some species have peduncles conspicuously covered with trichome-like glands, e.g., *P. squamicaule* (Fig. 384), *P. squamipetiolatum* (Fig. 388), and *P. verrucosum* (Fig. 440).

The peduncle is usually much narrower than the spathe, commonly no more that ⅓ to ¼ the width of the spathe tube, and is almost always broadened distally, merging almost imperceptibly with the spathe tube. Usually the color distinction is also gradual, but in some cases, e.g., *P. annulatum, P. dodsonii*, and *P. dolichophyllum*, there is an abrupt transition between the green peduncle and the colored spathe. In *P. ligulatum* there is a purple ring at the apex of the petiole, much like that at the apex of the petiole (Fig. 276).

The length of the peduncle, especially relative to the length of the spathe, may be important taxonomically. Some species, e.g., *P. antonioanum, P. crassispathum, P. davidsonii, P. ferrugineum, P. findens, P. malesevichiae, P. purulhense, P. radiatum, P. schottianum*, and *P. zhuanum*, have very short peduncles relative to the length of the spathe. In contrast, other taxa, e.g., *P. advena, P. angustilobum, P. dodsonii, P. hebetatum, P. heleniae, P. immixtum, P. mexicanum, P. pterotum, P. rothschuhianum*, and *P. wilburii* var. *wilburii*, have peduncles as long as or longer than the spathes.

Peduncles range in length from 1 to 25 cm, with

four taxa, *P. microstictum*, *P. pseudauriculatum*, *P. wilburii* var. *longipedunculatum*, and *P. verrucosum*, all having peduncles that attain the maximum length of 25 cm. Several additional species have peduncles that may be more than 20 cm long. These include *P. anisotomum*, *P. brunneicaule*, *P. panamense*, *P. pseudauriculatum*, *P. rothschuhianum*, and *P. scalarinerve*.

Many species of *P.* subg. *Philodendron* have peduncles more than 10 cm long. In addition to those mentioned above, 37 Central American species have peduncles more than 10 cm long, while 38 taxa (35 species) have peduncles less than 10 cm long. Sixteen species have petioles that may be less than 3 cm long, but only *P. knappiae* has a peduncle which does not exceed 3 cm in length.

SPATHES

The spathe of *P.* subg. *Philodendron* is highly variable in many regards. The spathe of *Philodendron* is typically coriaceous and constructed in such a way that the spathe may open and reclose without major alteration in its shape. The margins are invariably much thinner, with the apical portion of the spathe usually tightly rolled and frequently acuminate (Fig. 178, *P. findens*) and the basal portion more conspicuously convolute. Because the margins of the base are more conspicuously overlapped, when the spathe opens the lower portion remains convolute (Fig. 70, *P. auriculatum*) whereas the apical portion separates to very near the tip. Some species have spathes that open more fully so that the opening is almost rounded (Fig. 298, *P. panamense*) or broadly elliptic (Fig. 288, *P. mexicanum*). In such cases more of the inner tube surface and the pistillate portion of the spadix are exposed. On the other hand, some species have spathes that open only slightly so the opening is merely elliptic with the pistillate portion of spadix not visible without peering down through the top of the opening (Fig. 63, *P. antonioanum*).

Species vary greatly in the extent to which the spathe remains convolute at the base during anthesis. Spathes of some species, e.g., *P. angustilobum* (Fig. 51) and *P. mexicanum* (Fig. 288), unfold to very near the base. Those of other species, e.g., *P. antonioanum* (Fig. 63), do not open very broadly. The spathe tubes of *P. auriculatum* (Fig. 70), *P. panamense* (Fig. 298), and *P. wendlandii* (Fig. 451) remain convolute only in the lower half. The spathe of *P. davidsonii* (Figs. 134, 136) may be convolute only in the lower ⅓ to ⅔ in *P. squamicaule*. That of *P. hebetatum* (Fig. 226) is convolute to the upper ¼ and the spathe tubes of *P. aromaticum* (Fig. 68), *P. brenesii* (Fig. 89), *P. copense* (Fig. 110), *P. scalarinerve* (Fig. 140), *P. findens* (Fig. 177), *P. rothschuhianum* (Fig. 340), *P. straminicaule* (Fig. 360), and *P. schottianum* (Fig. 371) remain essentially closed to the apex of the tube during anthesis.

Mayo (1986) presented a classification of inflorescence types based principally on South American *Philodendron* species. Eleven inflorescence types were characterized, and a key was prepared to separate them. The characters chosen for use in the key were: (1) presence or absence of resin ducts in the inner surface of the spathe; (2) solitary vs. two or more inflorescences per axil; (3) relative length of the sterile staminate portion of the spadix (equal to or longer than the staminate portion vs. shorter than staminate zone); (4) presence or absence of colorful contrasts on inner surface of spathe tube; (5) prominently constricted vs. weakly constricted spathes; (6) presence or absence of resin ducts in the spathe; (7) presence of resin ducts in the sterile staminate portion of spadix vs. with resin ducts in either the fertile staminate portion or in both sterile and fertile staminate portions; (8) presence of non-functional resin canals in the spathe vs. resin canals lacking in the spathe (usually correlated with contrasting spathe colors); and (9) presence or absence of a terminal sterile zone on the spadix.

While I believe that this classification may be somewhat artificial, it demonstrates many evolutionarily important morphological features and shows the complexity of the *Philodendron* spathe.

Species of *P.* subg. *Philodendron* have the spathe tube relatively well demarcated from the blade either by being constricted at the apex or by its contrasting color. Some species, e.g., *P. crassispathum* (Fig. 124), lack any constriction above the tube, thus the spathe is more or less elliptic. Species that have a weakly constricted spathe include *P. advena* (Fig. 40), *P. alticola* (Fig. 45), *P. breedlovei* (Fig. 85), *P. purulhense* (Fig. 323), *P. schottianum* (Fig. 368), and *P. antonioanum* (Fig. 63). Despite these exceptions, most members of *P.* subg. *Philodendron* have spathes to some extent constricted. The subgenera *Meconostigma* and *Pteromischum*, on the other hand, have spathes not likely to be constricted or are only weakly constricted (Mayo, 1986).

Spathe length is relatively variable depending on the age of the plant and the stage of development. Elongation of the spathe is typically more or less arrested after anthesis, but sometimes a considerable amount of elongation takes place in both the peduncle and spathe after anthesis, presumably to accommodate the considerable expansion of the developing fruits. Spathe length varies from as little

as 4.5 cm in *P. clewellii* and 4.8 cm in *P. heleniae* to 29 cm in *P. pterotum* and 30 cm in *P. warszewiczii.* Relatively few species have spathes that ever exceed 25 cm in length even when in fruit.

Relatively few species have spathes less than 10 cm long. These are: *P. brewsterense, P. chirripoense, P. clewellii, P. dwyeri, P. knappiae, P. roseospathum* var. *angustilaminatum,* and *P. ubigantupense.*

The shape of the spathe and the relative disposition of the spadix at anthesis are taxonomically significant, but seldom described. This is because many species are still poorly known at anthesis, no doubt due to the fact that anthesis in *Philodendron* lasts only one or two days for each inflorescence.

One of the features that determines the shape of the spathe at anthesis is the degree to which the spathe opens. Spathes of some species, such as *P. aromaticum, P. copense, P. dodsonii, P. findens, P. fragrantissimum, P. grandipes, P. hebetatum, P. jodavisianum, P. straminicaule,* and *P. strictum,* open along the blade portion (see discussion above), leaving an oblong-elliptic opening (Fig. 110, *P. copense*; Fig. 140, *P. dodsonii*; Fig. 378, *P. smithii*). In these examples the spadix is either included within the spathe or is barely exserted, stiffly erect yet held slightly in front of the top edge of the spathe. On the other hand, spathes of some species, such as *P. angustilobum, P. mexicanum,* and *P. tripartitum* (Fig. 423), may open so broadly as to expose much of the pistillate portion of spadix. The pistillate portion of the spadix is usually for the most part obscured by the prominently convolute tubular portion of the spathe, as in *P. antonioanum, P. aromaticum, P. copense,* and *P. dodsonii.* Those species with spathes opening more broadly may also have the spadix protruding forward somewhat out of the spathe (see section on Spadix).

The definition of the spathe tube is somewhat imprecise, in terms of both morphology and color, but the spathe tube may be defined as the lower portion of the spathe (that portion which covers the pistillate portion of the spadix). In reality it usually extends somewhat above the pistillate portion to include the lowermost or sterile zone of the staminate portion of the spadix. In cases where the spathe has an obvious constriction it is that portion below the constriction (the balance being the spathe blade) that is referred to as the spathe tube. Though the ending of the spathe tube is imprecise, it generally terminates where the greatest constriction of the staminate portion of the spadix occurs, usually immediately above the sterile staminate portion of the spadix. Functionally, the constriction of the spathe, coinciding with the narrowest portion of the staminate portion of the spadix, prevents much of the pollen from the fertile upper portion of the spadix from falling directly into the chamber of the pistillate portion of the spathe. This probably serves more to prevent wastage of the pollen (by containing the pollen in a place where it can most easily be carried away by beetles) than it does to prevent self-pollination, since most species are so markedly protogynous that no self-pollination is possible, i.e., the pistils are probably no longer receptive when the pollen is shed. Testing for pistil receptivity with the use of peroxidase paper, Grayum (1996) found stigmas receptive throughout the period of staminal dehiscence in *P.* subg. *Pteromischum,* but numerous attempts at self-pollinations of members of *P.* subg. *Philodendron* by me and others failed to produce berries and instead resulted in aborted inflorescences. Not surprisingly those species, e.g., *P. advena, P. crassispathum* (Fig. 124), and *P. purulhense,* that have spathes scarcely constricted above the tube also have spadices not markedly narrowed above the sterile staminate flowers. It is not known whether the pollination behaviors of these species differ.

For *Philodendron* species with a prominent spathe constriction, the partially closed spathe during staminal anthesis, coupled with the swollen area of the staminate portion of the spadix immediately below it, provides a "pollen well" through which the beetles must squeeze on their departure. This probably ensures a greater coverage of pollen for the departing beetle pollinators.

Spathe tube shape and length are not particularly useful taxonomically. Tubes range in shape from virtually oblong (e.g., in *P. heleniae, P. ligulatum,* and *P. tripartitum*), to oblong-elliptic (e.g., in *P. aromaticum, P. copense, P. dodsonii, P. findens, P. gigas, P. hebetatum,* and *P. pseudauriculatum*) to elliptic (e.g., *P. rothschuhianum* and *P. smithii*), and range from only 2 cm long in *P. clewellii* to 14 cm long in *P. davidsonii* and *P. warszewiczii.* Species with spathe tubes longer than 10 cm are: *P. auriculatum, P. ferrugineum, P. schottianum, P. sousae,* and *P. tysonii.* Seventeen species have spathe tubes less than 5 cm long.

Even though the spathe tube often remains totally closed at anthesis it is, nonetheless, still somewhat expanded owing to the separation caused by the flaring of the spathe blade. Generally this provides considerable room around the spadix to accommodate the pollinating beetles (Figs. 100, 128, 242, 268). At anthesis the spathe tube is considerably more voluminous than before anthesis.

Spathe color. Spathe coloration is generally taxonomically significant though variable depending on

the age of the inflorescence. Before anthesis spathes are frequently green on the outside, but reddish coloration often develops well in advance of anthesis. Coloration of the spathe tube and blade often differs, with the spathe tube more commonly various shades of green and the spathe blade more commonly white, whitish, or whitish green. Even when the spathe is green throughout, the spathe blade is typically paler green than the tube. The tube portion of the spathe is commonly colored or tinged with red, maroon, or purplish violet (sometimes with other shades of red, orange, or purple) on one or both surfaces. Strong color contrasts (other than merely green vs. white), so common in *Philodendron*, are absent in other ostensibly related genera, namely *Furtadoa*, *Homalomena*, and *Anubias* (based on the *Philodendron* Alliance of Mayo, Bogner & Boyce, 1995) and also *Cercestis* and *Culcasia* (included in the *Philodendron* Alliance of Grayum, 1990). This would also be true of other presumed relatives including *Dieffenbachia*, *Montrichardia*, *Nephthytis*, *Peltandra*, *Typhonodorum*, and even *Zantedeschia*.

Generally if the spathe is colored on the outer surface it is also colored on the inner surface (but the reverse is not true). The inner surface is typically much more intensely colored than the outer surface. The coloration of the inner surface of the spathe, though commonly more or less restricted to the tube, may extend well onto the blade, sometimes even to very near the apex, such as in *P. breedlovei*, *P. davidsonii*, *P. mexicanum*, and sometimes *P. sagittifolium*. In some cases, such as *P. findens* and *P. schottianum*, the color is merely weakly diffused onto the inside of the blade. At other times only the very base of the tube is colored inside, such as in *P. ligulatum* and *P. hederaceum*. The spathe blade is commonly more extensively colored on the outer than on the inner surface, although blade coloration is highly variable, both inter- and intraspecifically. Nevertheless, most species have spathe blades some shade of green or white on the outer surface, often tinged with red, pink, purple, or yellow. A few species, such as *P. sagittifolium* and *P. ferrugineum* (Fig. 167), have purplish spots or blotches throughout much of the exterior of the spathe surface. Although the external coloration of the spathe is usually restricted to the tube portion, it often extends onto the blade, a situation that happens more frequently on the outer surface of the spathe than on the inner surface. Species that have coloration extending well above the spathe tube are: *P. antonioanum*, *P. breedlovei*, *P. dolichophyllum*, *P. subincisum*, and *P. roseospathum*. Sometimes the coloration of the spathe may be restricted to the tube, but only near the margins of the open edge such as in *P. grayumii* and *P. malesevichiae*.

While some species, e.g., *P. alticola*, *P. heleniae*, and *P. findens*, show little or no distinction in the coloration of the spathe tube and spathe blade, other species have distinctly different colors. In some cases, e.g., *P. antonioanum*, *P. cretosum*, *P. edenudatum*, *P. findens*, *P. grandipes*, *P. lazorii*, *P. ligulatum*, *P. llanense*, and *P. roseospathum*, the transition from one color to the next is very gradual. In other cases, such as *P. hebetatum*, *P. immixtum*, *P. jodavisianum*, *P. panamense*, *P. pterotum*, *P. strictum*, *P. radiatum*, *P. rothschuhianum*, *P. scalarinerve*, *P. smithii*, *P. tenue*, *P. wendlandii*, and *P. zhuanum*, the transition is less gradual but by no means abrupt. Still other species, e.g., *P. ligulatum* var. *ovatum*, *P. dodsonii*, *P. gigas*, *P. strictum*, and *P. fragrantissimum*, show a distinct and abrupt transition in the spathe tube and blade colors.

The biological significance of the frequently darker colors on the inside of the spathe tube in contrast to the paler colors of the spathe blade is uncertain. It seems unlikely that either the contrasting colors or the dark color of the spathe tube act in attracting pollinators. The presumed pollinators, dynastine scarab beetles (see section on "Pollination Biology"), are believed to orient more by smell than sight (Faegri & van der Pijl, 1979; Gottsberger & Silberbauer-Gottsberger, 1991). Moreover, their normal arrival time, near dark, would probably preclude their seeing contrasting colors in any event. In addition, the dark coloration is usually restricted to the spathe tube and often not even visible in good light from near the mouth of an open spathe. It is more likely that the dark-colored spathe tube acts to encourage these crepuscular beetles to stay for an extended period of time. Mayo (1986) pointed out that, since neither *P.* subg. *Pteromischum* nor *P.* sect. *Meconostigma* have color contrasts in the spathe blade and tube, *P.* subg. *Philodendron* may have different pollinators. Although not enough pollinators have yet been identified to confirm this possibility, there seems to be little evidence in favor of Mayo's hypothesis (see section on "Pollination Biology"). Some beetle species, such as *Erioscelis proba* Sharp, are known to visit species of both *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* (Grayum, 1996) (see also Table 3, "Pollinators of *P.* subg. *Philodendron*").

Lenticel-like structures on both the exterior of the spathe tube and the peduncle in some *Philodendron* species secrete large droplets of a viscous, somewhat sweet substance. Mayo (1986) has shown that these may consist of clusters of stomata, and

Table 3. Pollinators of *Philodendron* subg. *Philodendron*.

Plant species	Voucher	Beetle species
P. anisotomum		**Cyclocephala amblyopsis* Bates
		**Erioscelis columbica* Endrödi
P. brenesii	*Croat 35519*	*Cyclocephala nigerrima* Bates
P. brevispathum		*Erioscelis proba* Sharp
P. callosum	No voucher	*Cyclocephala rustica* (Olivier)
P. correae	*Croat 66653*	*Cyclocephala conspicua* Sharp
P. grandipes	*Croat 76594*	**Cyclocephala gravis* Bates
	Jiménez 6	*Cyclocephala sexpunctata* Castelnau
	Jiménez 6	*Erioscelis columbica* Endrödi
	Croat 43289	
P. grayumii	*Croat 74840*	*Cyclocephala rubescens* Bates
	Croat 74840	*Cyclocephala sexpunctata* Castelnau
P. jodavisianum	*Croat 35950*	*Cyclocephala ligyrina* Bates
	Croat 35950	*Cyclocephala mafaffa* Burmeister
		**Erioscelis columbica* Endrödi
P. ptarianum	*Ramírez 1163*	*Cyclocephala rustica* (Olivier)
P. pterotum		**Cyclocephala ampliata* Bates
		**Cyclocephala amblyopsis* Bates
	Croat 10903	*Cyclocephala ligyrina* Bates
		**Cyclocephala sexpunctata* Castelnau
P. radiatum		**Cyclocephala ampliata* Bates
		**Erioscelis columbica* Endrödi
		**Cyclocephala amblyopsis* Bates
		Cyclocephala ligyrina Bates
		Cyclocephala kaszabi Endrödi
P. rothschuhianum		**Cyclocephala amblyopsis* Bates
	(Young, 1987)	*Cyclocephala kaszabi* Endrödi
		**Erioscelis columbica* Endrödi
P. sagittifolium	*Thompson 4636*	*Cyclocephala sexpunctata* Castelnau
P. schottianum	*Croat 36110*	*Cyclocephala melane* Bates
P. tripartitum		**Cyclocephala amblyopsis* Bates
		**Cyclocephala kaszabi* Endrödi
		**Erioscelis columbica* Endrödi
P. tysonii	*Croat 66711*	*Cyclocephala nigerrima* Bates

*Entries were provided by Helen Young, Barnard College, New York, and were based on unpublished observations made during 1984–1985 at La Selva (O.T.S. Field Station) in Costa Rica (with the assistance of George Schatz). Entries without an asterisk were based on determinations made by John Rawlins at Carnegie Museum in Pittsburgh. Collections by S. Thompson were contributed independently to Rawlins.

pointed out their possible ecological significance as extrafloral nectaries.

The secretion of resin from the inner surface of the spathe is apparently unique, in Araceae, to *Philodendron* (Mayo, 1991). Mayo (1986) enumerated four different types of inflorescence resin canals, at least two of which occur among Central American *Philodendron*. One type, found in *P. tripartitum*, has large-diameter resin canals imbedded just beneath the epidermis on the inner surface of the spathe. Resin is secreted directly onto the surface. Another type, represented by *P. smithii*, lacks resin canals on the spathe but instead has resin canals in the staminate zone of the spadix.

The two other types of resin canals pertain to *P.* subg. *Meconostigma* and *P.* subg. *Pteromischum*. In the former, exemplified by *P. bipinnatifidum* Schott ex Endl., the resin canals are "J"-shaped and tangential, arising in the aerenchyma of the spathe and extending to the surface. In the latter, exemplified by *P. sonderianum* Schott, the resin canals are evenly distributed between the aerenchyma and epidermis and are parallel to the surface of the epidermis rather than arising in a J-shaped fashion.

Resin canals usually are present in the proximal ½ to ⅔ of the spathe blade and sometimes also the distil portion of the tube. In *P.* subg. *Philodendron*, these resin canals are generally reddish, red-pur-

ple, or orange to brownish and generally somewhat intermittent, as in *P. sulcicaule*, though sometimes continuous, as in *P. immixtum*, *P. mexicanum*, *P. sagittifolium*, and *P. wilburii*. They are always oriented vertically, paralleling the veins of the spathe. The resin canals actively secrete a resinous liquid at anthesis that wells up onto the surface of the spathe and sometimes runs down the spathe below the resin ducts. The resin is generally very sticky and probably functions in causing pollen, sometimes itself not particularly sticky, to adhere to the bodies of the beetle pollinators as they leave the spathe.

SPADIX

Philodendron species are monoecious, with the spadix bearing naked unisexual flowers. The flowers lack a perigon and are closely arranged on a more or less cylindrical spadix, with the staminate flowers comprising the upper ⅔–⅘ of the spadix and the pistillate flowers comprising the remaining basal portion. The average spadix for *P.* subg. *Philodendron* in Central America has the staminate portion 2.2 times longer than the pistillate.

The spadix is usually contained for the most part inside the spathe at anthesis (see section above on the Spathe), although in the majority of species the spadix is weakly exserted in front of the spathe. The majority of plants at anthesis have their spathes erect or tipped slightly forward so they can provide shelter to spadices from water dripping straight overhead.

Spadices of some species, especially those with broadly opened spathes (e.g., *P. angustilobum* (Fig. 51), *P. ligulatum* (Fig. 266), *P. mexicanum*, and *P. tripartitum*) protrude prominently forward at anthesis. Other species whose spathes remain convolute to about the middle may also have spadices that protrude prominently forward; these are: *P. auriculatum*, *P. davidsonii*, *P. grayumii*, *P. hebetatum*, *P. heleniae* (Fig. 229), *P. jodavisianum*, *P. ligulatum*, *P. llanense* (Fig. 268), and *P. panamense* (Fig. 299).

The spadix of *Philodendron* is usually only slightly shorter than the spathe. The average length of the spathe is 16.5 cm, while the average spadix is 15.8 cm long. Thus on average, the spathe is nearly 1 cm longer than the spadix. This difference may be as little as a few millimeters or as much as 4 cm.

The general morphology of the spadix of *Philodendron*, though highly variable in detail, is more or less the same for all species in Central America. The pistillate portion is usually pale green to greenish white and obliquely attached to the spathe, and sometimes markedly stipitate at the base. The floriferous part of the spadix is thus longer on the adaxial (front) than on the abaxial (back) surface (Fig. 40). The differences in the length of the adaxial and abaxial surfaces of the pistillate portion of the spadix depend on the angle at which it is attached to the spathe. These are referred to as "front side" and "back side" of the spadix in the descriptions presented in this revision.

The staminate portion of the spadix characteristically has a swollen sterile section at the base. Typically the staminate portion is broadest at the sterile section and gradually constricted just above this. Above the constriction the spadix is fertile and is gradually broadened usually to a point about ⅔ of its length, then narrowed gradually or abruptly to the tip.

The staminate portion is usually uniformly white to creamy white on the outside, although sometimes with the axis pinkish. Immature spadices are usually green, though they become white well before anthesis. The sterile section of the staminate portion is commonly a different color than the fertile section. Often it is more nearly white at an earlier stage of development when the fertile flowers are typically green. At anthesis the sterile staminate portion is more likely to be tinged with yellow or tan, reflecting the higher concentration of oil in these flowers than in the fertile flowers (see below). However, sometimes at anthesis the sterile and the fertile staminate flowers are identical in color. The sterile staminate portion frequently can be distinguished easily after anthesis with the sterile portion maintaining a white color (Fig. 28) while the fertile portion turns grayish or brownish. The sterile staminate portion can usually be distinguished even in these cases by the difference in the size of the spadix (usually larger than the adjacent fertile staminate portion), by the usually larger and more irregularly shaped flowers, and because the sterile staminate section typically ends just before the narrowly constricted portion of the fertile staminate portion (which itself coincides with the constricted portion of the spathe). The sterile staminate flowers are often more easily discernible on dried specimens than they are on live ones since they tend to dry a different color, usually somewhat more brownish.

The much higher oil content of the sterile staminate flowers was reported by Pohl (1932), and it is probably owing to this high oil content that the sterile staminate flowers are often eaten by the beetle pollinators (Fig. 29). A high concentration of

lipids in the mitochondria of the staminodial cells has been documented (Walker et al., 1983).

The fertile staminate portion of the spadix is typically more or less clavate and bluntly tapered toward the apex. In a few species, such as *P. advena*, *P. crassispathum*, and *P. davidsonii*, it is more nearly oblong-ellipsoid, often broadest at the base and bluntly tapered toward the apex. The spadix of *P. ferrugineum* is similarly shaped but is somewhat more constricted above the sterile staminate portion. Some species, e.g., *P. heleniae*, have the spadix broadest in the upper ⅓ rather than in the sterile staminate portion.

Male flowers. The androecium of *P.* subg. *Philodendron* is truncate at the apex, prismatic to obpyramidal and usually irregularly 4–5-sided (Fig. 30). It consists of 2–6 sessile stamens (mostly 3–4). These are always distinct for most of their length although often weakly fused at the base. Stamen number varies within a single spadix and is never constant (Mayo, 1986). Despite the clear grouping of stamens it is sometimes difficult to discern clear floral groupings, especially when the stamens are distinct. Mayo (1986) reported that some species have stamens dehiscent laterally rather than extrorsely.

The androecia in *P.* subg. *Philodendron* range from 2 to 6 mm diam. and show little interspecific variation. Stamens of all species studied by Mayo (1986) had druses in their apices. Anthers are sessile to subsessile with a thick connective that is truncate at the apex and overtops the thecae. The connective of all species studied by Mayo (1986) had raphides present. The thecae are ellipsoid, oblong or linear, emarginate at the base, and each opens by a short lateral slit or subapical pore. The two thecae of a stamen are generally adjacent in *P.* subg. *Philodendron* but positioned far apart in *P.* subg. *Pteromischum* and *P.* subg. *Meconostigma.* Anther thecae lack cell wall thickenings in the endothecium in *P.* subg. *Philodendron* (French, 1985).

Pollen typically emerges in long, slender, somewhat viscid filamentous strands (Fig. 31) (see section on "Pollination" for a description of its emergence). These slender strands of pollen do not persist for many hours, and ultimately the pollen becomes matted in irregular clusters (Fig. 391, *P. straminicaule*).

In *P.* subg. *Philodendron* resin canals in the staminate portion of the spadix are situated beneath the stamens and secrete resin onto the surface of the stamens. The same is not true of *P.* subg. *Pteromischum* and *P.* sect. *Meconostigma*, where the resin canals are borne at a deeper level in the axis and do not secrete resin onto the surface of the stamens (Mayo, 1986) (Fig. 128, *P. crassispathum*).

French (1986a) reported that the stamen vasculature of most species of *P.* subg. *Philodendron* consists of a single forked bundle with widely divergent branches. Carvell (1989) reported that a single unbranched trace supplies each stamen. According to Mayo (1986) the staminodia have a more distinctive floral receptacle than do the fertile staminate flowers and often have a multiple-branched vascular trace, whereas the latter have an indistinct floral envelope and only a once-branched vascular trace. In contrast, members of *P.* subg. *Meconostigma* have traces that lack branches or have only short branches that spread at an acute angle.

Stamens in *P.* subg. *Philodendron* have both druses and raphide idioblasts with secondarily thickened walls and tanniniferous idioblasts occurring throughout the ground tissue (Carvell, 1989).

POLLEN

Anthers of *Philodendron* (Grayum, 1991) have a two- or more-layer tapetum of a periplasmodial type. Pollen mother cell cytokinesis is probably successive.

Philodendron pollen (Fig. 30) is binucleate (Zavada, 1983; Grayum, 1985, 1986, 1992a), inaperturate, starchy and of moderately large size (averaging 40 μm, ranging 28 μm–40 μm), with subisopolar polarity (Grayum, 1985, 1991). As in most aroid genera, it is shed in monads. Pollen is typically boat-shaped-elliptic to oblong, or occasionally elongate as in *P. radiatum.* It is usually round in cross section, but may be very obscurely keeled in *P. hederaceum* to moderately keeled in *P. jacquinii, P. jodavisianum,* and *P. wendlandii,* or prominently keeled in *P. mexicanum.* The exine sculpturing is usually psilate, but sometimes minutely verruculate, scabrate, or fossulate (*P. fragrantissimum, P. grandipes, P. jacquinii, P. jodavisianum,* and *P. pterotum*) to punctate, subfossulate, subfoveate, or subverrucate (*P. mexicanum* and *P. wendlandii*).

FEMALE FLOWERS

The pistils of *P.* subg. *Philodendron* are closely aggregated on the spadix in a series of irregular spirals. Gynoecial characters have long been considered important in the subgeneric classification of *Philodendron,* and lobed stigmas were used as early as 1832 by Schott in the recognition of his greges *Meconostigma* and *Sphincterostigma* (the latter now a synonym of the former). The number of

ovules per locule was used by Engler (1878) in part to characterize the two largest sections of the genus, *Oligospermum* Engl. and *Polyspermium* (now *Calostigma* and *Philodendron*, respectively) (Mayo, 1990).

The pistillate flowers consist of a single naked pistil lacking staminodia. Typically the ovaries are ovoid to obovoid or elliptic, and terete in cross section, or with the sides often somewhat irregularly angular by compression owing to their close proximity with adjacent pistils. Embryo sac development is of the *Polygonum*-type (Grayum, 1991). Each ovary for the genus is syncarpous, superior, and contains 2–47 locules (4–10 in *P.* subg. *Philodendron* of Central America). Ovaries range in size from 0.5 mm (as in *P. sousae*) to 9.2 mm long (as in *P. advena*). The locules are typically oblong, with thin translucent walls that extend ⅔–¾ the length of the ovary. The style is barely distinguishable from the remainder of the ovary, mostly by being slightly thicker and opaque, rather than translucent. While Dahlgren and Clifford (Dahlgren et al., 1985) reported no style in Araceae, both Eyde et al. (1967) and Mayo (1986, 1989) indicated that the region has a distinct anatomy. Mayo (1989) defined the style of *Philodendron* as "that portion of the gynoecium between the base of the stigmatic epidermis and the ovary locules." Slender, conspicuous styles are rare in *Philodendron*, but do exist, as in *P. jacquinii* (Fig. 242).

Each carpel is connected to the stigma apex or compitum (common stylar canal) by a stylar canal. The compitum (Endress, 1982) is a cavity or complexly shaped channel into which the pollen may be inadvertently packed by the beetle pollinators. This no doubt allows for enough grains to be left to insure pollination, and to make sure not all are removed from the stigma by movements of the beetles. The stigmatic epidermis extends into the compitum from the stigma apex (Mayo, 1989). At the base of the channel or cavity there is a ring of holes that leads into the stylar canals. Where no compitum is present, such as with "Type B" and "Type D" styles (see section on "Style Types" below), the stylar canals lead directly onto the surface of the style. These canals are readily visible on the dried stigmas of many species if the preservation is adequate. They are particularly easy to see in fruiting collections.

The gynoecium has a separate stylar canal for each carpel (see fig. 1 in Mayo, 1989). Each canal may open at its upper end into a compitum. A compitum is rare among Central American species (see section on Style Types below), but is present in *P. correae*, *P. ligulatum* var. *heraclioanum*, *P. smithii*, *P. straminicaule*, and *P. warszewiczii*. A compitum has also been seen on an unusual collection of *P. radiatum* and some populations of *P. tripartitum*.

The vascular anatomy of *Philodendron* ovules has been studied by French (1986b). Of the five species he studied, three were South American while two, *P. jacquinii* ("*P. hederaceum*") and *P. inconcinnum* ("*P. immixtum*"), occur in Central America. French reported a single vascular trace for all of these except *P. jacquinii*, which has multiple traces. Carvell (1989) reported that the vasculature of the gynoecium in *Philodendron* arises from a single trace, which divides centrifugally to yield a single branch trace for each locule. The carpel traces branch once to form a connection with the placenta as well as a single dorsal trace. The placental trace forms individual connections with each ovule (Carvell, 1989).

Finally, a few miscellaneous anatomical features of the gynoecium should be mentioned. Both tanniniferous idioblasts as well as raphide idioblasts are lacking in the gynoecium of *Philodendron*, but the gynoecium does contain druse idioblasts (Carvell, 1989). Like most Araceae, *Philodendron* has unicellular ovular and placental trichomes (French, 1987b). These function in secreting mucilage presumably for the protection of ovules.

Ovules of *Philodendron* are bitegmic, with the inner integument forming the micropyle. The integuments are usually completely free from one another (Grayum, 1991).

Seemingly the most important morphological features of the pistil from the standpoint of systematic importance are the quantity and distribution of the ovules and the type of style, discussed in subsequent sections.

Placentation. Placentation type for *P.* subg. *Philodendron* in Central America is usually axile or sub-basal, with 50 species having sub-basal placentation and five species with basal placentation. Those with basal placentation are: *P. dwyeri*, *P. granulare*, *P. smithii* (also sometimes sub-basal), *P. sousae* (also sometimes sub-basal), and *P. zhuanum*. Forty-seven species have axile placentation and two additional species, *P. ferrugineum* and *P. sagittifolium*, with mostly sub-basal placentation, sometimes have axile placentation when they have especially numerous ovules per locule.

Some general rules regarding placentation type and number of ovules per locule are the following: species with basal placentation have only a solitary ovule per locule and tend to have a few large seeds per berry. Species with sub-basal placentation usually have only 1 to a few ovules per locule (aver-

aging 2.1 to 3.5 respectively for the minimum and maximum number in the range) and typically fewer than 6 but rarely to 10 or to 12 (as in *P. brenesii* and *P. davidsonii* subsp. *bocatoranum*). Species with basal and sub-basal ovules tend to have rather large seeds as well, although sometimes their seeds are quite small. On the other hand, species with axile placentation usually have 10 or more ovules per locule (averaging 14–18 respectively for the minimum and maximum in the range) but sometimes as few as 3 (*P. dressleri* and *P. warszewiczii*), or 4.

For those species with only a few ovules per locule, the disposition of the ovules seems to be unorganized or digitate, but for those with more than a few ovules, the placentas may be uniseriate or more generally biseriate or, less frequently, in 1–2 or 2–3 series (see Appendix 2, "Technical Data on Pistils"). Mayo (1989) reported that, based on his studies of the gyneocial morphology and anatomy of 15 mostly South American *Philodendron* species, the placenta of even those species whose ovules appear to be in a single row might actually be biseriate, with the funicles inserted alternately along the placental ridge. This is also true in Central American species. Forty Central American taxa of *Philodendron* proved to have biseriate placentas, while much smaller numbers appeared uniseriate (13), 1–2-seriate (9), 2–3-seriate (11), or digitate (4). Twenty-six species lacked any appreciable organization owing to the small number of ovules, and one species, *P. niqueanum*, was not studied due to inadequate material.

Ovary locule number. Mayo (1991) reported that ovaries in *P.* subg. *Meconostigma* range from 3- to 47-locular, and Bunting (1986) reported 2 (rarely 3) locules per ovary as characteristic of *P.* sect. *Philopsammos.*

Though the number of ovules per ovary is highly significant in separating *P.* sect. *Philodendron* and *P.* sect. *Calostigma*, the number of locules is not a good indicator of relationship. While the average number of locules per ovary has a slightly lower range for *P.* sect. *Philodendron* (4.6–6.1 vs. 5.5–7.4 for *P.* sect. *Calostigma*), the difference is not great. In *P.* sect. *Calostigma* the number of locules per ovary ranges from 1 to 10. In *P.* sect. *Philodendron* it ranges from 3 to 10. While *P.* sect. *Philodendron* rarely has more than 8 locules per ovary, and *P.* sect. *Calostigma* rarely has fewer than 5, more species (14 in all) have 8 locules per ovary than any other number.

No species of *P.* subg. *Philodendron* in Central America were found to have bilocular ovaries, though two species, *P. sagittifolium* and *P. zhuanum*, may have only a single locule. In the latter species, the number of locules ranged only from 1 to 3, but in *P. sagittifolium* the number of locules ranged up to 8. Often such low locule numbers occur only near the base of the spadix, where the ovaries are often somewhat irregular in shape. Frequently, the lowermost pistils on the spadix are larger or smaller than those in the middle of the spadix and are more widely spaced and of irregular cross-sectional shape. Three-locular ovaries are rare, known only in two species: *P. copense* and *P. sagittifolium.* Five other species, *P. chirripoense, P. hederaceum, P. immixtum, P. morii,* and *P. squamicaule,* may rarely have 3-locular ovaries.

Four-celled ovaries are fairly common in *P.* subg. *Philodendron.* Four species, *P. cretosum, P. jacquinii, P. knappiae,* and *P. subincisum,* so far have demonstrated only 4-locular ovaries. Most species with 4-locular ovaries also have 5-locular ovaries on the same spadix. Four species showed exclusively 5-locular ovaries. Only eight species have locule numbers greater than 10; all but one of these are in *P.* sect. *Calostigma.*

Ovules per locule. The number of ovules in each locule varies from 1 to numerous. Mayo reported numbers as high as 51 for *P.* subg. *Meconostigma,* but my studies of *P.* subg. *Philodendron* show the highest number found for any Central American species is 36, in *P. fragrantissimum.* Only 4 other species, *P. antonioanum, P. panamense, P. squamipetiolatum,* and *P. verrucosum,* have 30 or more ovules per locule, and 17 species have 20–29 (see Appendix 2, "Technical Data on Pistils"). Fifty-six species (62 taxa) have fewer than 10 ovules per locule.

Along with leaf morphology, the number of ovules per locule has long been used as a principal means of assigning sectional affinity in *Philodendron* (Engler, 1878, 1879, 1899; Krause, 1913; Mayo, 1989). Central American members of *P.* subg. *Philodendron* generally fall into three categories in terms of number of ovules per locule. Many species, including most members of *P.* sect. *Calostigma, P.* sect. *Tritomophyllum* and *P.* sect. *Baursia,* have one to few (rarely to 4 or 5, but always with basal or sub-basal placentation). Forty-four species and four subspecies belong to this category. A second group, with axile or sub-basal placentation, generally has 4–10 ovules per locule, but sometimes up to 14. Nineteen species fall into this category. The third group has exclusively axile placentation, mostly with many (15+) ovules per locule. These groups may not be natural, since two

species (*P. davidsonii* and *P. roseospathum*) have one variety in each of the aforementioned groups.

It might be expected that, since the pistils of different species of *Philodendron* are roughly the same size (mostly ranging from 1 to 4 mm long and about ½ to ⅓ as wide), the size of the ovules might be larger in those species with fewer ovules per locule than in those with more. Though there are differences in ovule size (see Appendix 2, "Technical Data on Pistils"), they are not great. Of 44 species of *Philodendron* studied that had axile placentation, the ovules ranged from 0.1 to 2.1 mm long. Alternatively, 48 species with basal or sub-basal placentation had only slightly larger ovules, ranging from 0.31 to 0.5 mm long.

Ovules in *Philodendron* are hemiorthotropous or orthotropous (Grayum, 1991), rarely hemianatropous (Mayo et al., 1997) and bilaterally symmetrical with an eccentric attachment of the funiculus (French, 1986b). The funicles are usually as long as or longer than the ovules. The ovules that are axile usually have funicles of different lengths, since they are positioned increasingly higher on the axis. After meeting with the wall of the locule the funicle is lightly fused to the wall all the way to the base and can be easily removed intact by pulling it free. This might argue against the assumption by Mayo (1989) that basal and sub-basal placentation were derived from axile placentation, since axile placentation could have developed by a lengthening of the funicular plexus and a fusion to the wall. While no anatomical study was made of this phenomenon, the frequent presence of basal funicles in axile placentas makes it appear that at least in the case of some Central American species of *P.* subg. *Philodendron*, species with axile placentation may have evolved from species with basal or sub-basal placentas.

The funicles in *P.* subg. *Philodendron* are frequently densely covered with short, usually inconspicuous, gland-like trichomes from near the base, sometimes extending to about half their total length. The secretory trichomes are continuous with those of the placentas and lining of the stylar canals (Mayo, 1989).

Funicles often bear a band of glandular trichomes at or near the base. These were well illustrated by Krause (1913) who reported them commonly in *P.* sect. *Baursia* and *P.* sect. *Calostigma* but with a few in *P.* sect. *Philodendron* as well. These small glands can only be seen under high magnification and probably secrete mucous into the ovary, preventing the ovules from drying out.

Funicles are often fused into a thickened, sometimes ramified, more or less translucent placenta. The entire placenta and its associated funicles and ovules may be removed, making counting them less difficult. Sometimes, however, adjacent locules share a common trunk so that care must be taken to insure that one is not removing the contents of two locules.

The free portion of the funicle on species with axil placentation seems to be proportionately shorter than the free portion of those with sub-basal placentation. This is perhaps because those species with axile placentation have somewhat longer locules allowing greater spacing of the ovules. Those species with sub-basal placentation and three or more ovules per locule have the funicles arising from one small area near the base of the axile wall, and often have much smaller locules than those with axile placentation. Ovules need to be separated for proper development, and funicles of different lengths allow for this. Thus, in many cases, funicles are longer in those species with sub-basal placentation. The generally smaller locule size for species with sub-basal or basal placentation is confirmed by a survey of locule size. Species with basal or sub-basal placentation have locules ranging in length from 0.32 mm in *P. jefense* to 9.5 mm in *P. warszewiczii*, with the average minimum length 1.9 mm and the average maximum length 3.5 mm. On the other hand, locules range in length from 0.40 (*P. bakeri*, *P. sousae*, *P. sulcicaule*, and *P. wilburii* var. *longipedunculatum*) to 0.7 mm (*P. advena*); the average minimum length is 1.12 mm while the average maximum is 1.75 mm.

The funicles of a single ovary are usually not of equal length if the ovules are basal or sub-basal, since the ovules are usually positioned at slightly different heights off the floor of the locule. Even when the ovules are scattered along much of the length of the axis of the locule wall, the funicles are of slightly different sizes.

Style and stigma morphology. This treatment follows the classification of styles and stigmas of Mayo (1989). Mayo (1986) defined the style in *Philodendron* as "that portion of the gynoecium between the ovary locules and the base of the stigmatic epidermis." Although there is considerable diversity at the microscopic level, much of the detail of the style is easily visible only by dissection (see section entitled "Style Types"). The fresh styles of *P.* subg. *Philodendron* are relatively uniform microscopically. Usually they are hemispherical or sometimes globose or depressed-globose. The microscopically visible portion is the stigma, a "single continuous area in which the epidermal cells are greatly elongated into secretory papillae" (Mayo, 1986). This

dense layer of stigmatic papillae is so closely packed and so engulfed in a gelatinous fluid as to appear almost solid. Still, a needle can be passed easily across and through much of its volume in any direction without disturbing its shape. The stigmatic papillae are slender, many times longer than broad, and attached to the surface of the style. Mayo (1986) reported that the stigmatic papillae often contain tannin cells.

The stigmatic papillae typically dry to form a thin, flat, often translucent, wafer-like mantle around the now somewhat visible style apex. In time the stigmatic mantle may fall off altogether allowing easy inspection of the style apex. Sometimes the stigma dries erect and disheveled. In these cases the appearance of the stigmas is more difficult to determine but, regardless of how the stigma dries, the style apex often can be made easily visible on a dried specimen by lightly scraping away the stigmatic papillae. The complexities of the style types of *Philodendron* are discussed below.

Style types. The present work adopts the gynoecial classification of Mayo (1989) in which six distinct style types were described and illustrated (Fig. 469, "Style Types in Central America"; see Appendix 2, "Technical Data on Pistils," which summarizes the style types for *P.* subg. *Philodendron* of Central America). Only two species, *P. niqueanum* and *P. utleyanum*, have style types not yet known. The table also includes the number of locules per ovary, placentation type, number of ovules per locule, ovary size, disposition of ovary, and the nature of the ovular sac when present.

Style type is one of the most important gynoecial features in *Philodendron.* While the stigma is moderately uniform in its superficial appearance, the style is highly diverse in morphological features. Unfortunately, these features are largely hidden by the stigmatic papillae when the pistil is fresh. Despite the shape of the style, the stigmatic papillae, which cover all or part of the style, may form a stigma of more or less uniform shape.

Style Type A has a compitum (common funnel into which the pollen may be packed, defined as the space between the upper stigmatic papillae and the level at which the stylar canals emerge onto the style surface) with ridged inner walls and a lobed apex, with each lobe corresponding to the apex of one carpel. Style Type A is restricted to *P.* subg. *Meconostigma* and thus will not be considered further here.

Style Type B (Fig. 469A) lacks a compitum. Instead, the stylar canals open into relatively broad concavities on the style apex. These concavities are arranged in a ring with one hole per locule. Style Type B also has the stylar canal entering directly into the apex of the locular cavity. Although the style apex may be completely flattened or broadly concave, it is sometimes weakly ridged between the apertures of the stylar canals. These ridges meet in the middle of the style and may even form a weak central beak. Some styles also have well-developed stigmatic papillae associated with the stylar canals causing the surface to be at least weakly lobed, with a single lobe for each locule. In dried condition Style Type B sometimes appears as a button-like structure, somewhat resembling Style Type D. It is therefore important in determining style type to make comparisons of material at or near anthesis. Style Type B seems to be most closely related to Style Type D and shares with that type the relatively large stylar canal pores on the surface of the style apex relatively near its periphery. Style Type B is the most common type in Central America, known in at least 70 species. One species, *P. tripartitum*, though usually having Type D styles, also has Type B and E styles in some populations of the species (see that species for a discussion of its style types).

Style Type C (Fig. 469B) is characterized by being decidedly concave or funnel-shaped at the apex with no lobes on the margins of the rim and with the stylar canals arising in a narrow cluster at the base of the compitum (funnel). Since the stylar canals are closely clustered there is no central dome (defined as any stylar tissue that lies above the level at which the stylar canals emerge onto the style surface). In contrast to style Types B and D, both of which have rather prominent stylar pores, the stylar pores of Type C are small, sometimes barely visible, and in a generally smaller circle nearer the middle of the style apex. This style type is rare in Central American *P.* subg. *Philodendron*, and is known primarily in *P.* subg. *Pteromischum.* Only five taxa of *P.* subg. *Philodendron*, (*P. correae*, *P. cotonense*, *P. ligulatum* var. *heraclioanum*, *P. straminicaule*, and *P. warszewiczii*) have exclusively Type C styles. Though their pistils are funnel-shaped at the apex, these species have funnels generally not as deep as those of *P.* subg. *Pteromischum* as illustrated by Mayo (1989). One other species, *P. radiatum*, has at least one collection (*Croat & Hannon 63414*) with the

style type that also has a funnelform apex and looks like a Type C style. While the dried style of this collection is distinct and button-like, the pores are central in a shallow concavity.

Style Type D (Fig. 469C) is similar to Type B in that it lacks a compitum and has thick stylar canals emerging in a circle on a flat stylar apex relatively close to the margin of the stigma apex. It differs from Type B in that the style is constricted around the circumference to form a protruded flat "style boss" (defined as a ± domed, circular, stigma-bearing projection that extends beyond the main part of the style and is separated from it by a short neck) that rises above the general level of the style apex. Thus the style appears to have a short flat neck at the apex. It is from the "style boss" that the stylar canals emerge. The stylar pores are relatively large and borne relatively near the margin of the style apex. At least 23 species of *P.* subg. *Philodendron* in Central America have Style Type D, the second most common style type.

It is easy to confuse or misinterpret Style Types B and D if the specimens are not well preserved, especially if the material studied is not fresh but rather rehydrated. Species with Type B styles sometimes have styles that dry with a button-like apex resembling that of Type D. At least one collection of *P. advena* has both Type D and Type B styles. Some populations of *P. tripartitum* have not only Type D styles but Type B and Type E as well (see the discussion of that species for details).

Style Type E (Fig. 469D) has a slender funnel-shaped to cylindrical compitum with a distinct raised annulus around the upper rim. The stylar canals arise in a small cluster at the base of the compitum just as in Type C styles. The latter differ, however, in lacking the rim on the style apex. Type E styles are rare in Central American *P.* subg. *Philodendron*, found in only *P. granulare* and perhaps *P. smithii*. *Philodendron granulare* has such an unusual form of the Type E style that it should perhaps warrant its own status. In *P. granulare* the annulus of the stylar funnel actually protrudes well above the surface of the style (at least in its dried state). *Philodendron smithii* was reported by Mayo (1989) as having a Type E style, but no rim is obvious in fresh material of the species. It is more appropriately a Type C style. *Philodendron tripartitum*, though usually with Type D styles, has Type E styles in some parts of its range (see the discussion following that species for details).

Style Type F is narrowly funnel-shaped with a small dome at the base of the compitum around which the stylar canals arise. This type is not known among the Central American *Philodendron*. It is known only from *P. burle-marxii* G. M. Barroso, a member of *P.* sect. *Baursia* (Mayo, 1989) from Amazonian Brazil.

Mayo (1989) has shown that the course of individual stylar canals is correlated with the type of placentation. Those species with basal or sub-basal ovules, such as *P. tripartitum* and *P. smithii*, have stylar canals that course down the center of the axis of the pistil and enter the locule near its base. Those species with axile placentation have stylar canals that also course down the pistil axis and enter the locule somewhere above the base of the locule, but only rarely at the very apex. The stylar canals are lined with papillose epithelial cells, which are contiguous with the stigmatic epidermis (Mayo, 1989). These secrete the gelatinous mucous that keeps the stigmatic surface moist.

FRUITS AND SEEDS

In *Philodendron* the developing pistils remain within the reclosed spathe after anthesis and pollination until they are fully ripe [except in the rare case of *P. surinamense* (Miq.) Engl., a South American member of *P.* subg. *Pteromischum* that promptly loses its spathe after anthesis]. The spathe enlarges somewhat to accommodate the enlarging berries. When the berries are mature the spathe once more begins the process of reopening, but it breaks completely free at the base where it is obliquely attached to the peduncle. Sometimes the spathe falls completely free after loosening even before it opens, but in general it breaks up beginning at the base and falls off (Fig. 33) eventually falling completely free and leaving a scar just above the peduncle (Fig. 34). Generally the old, withered staminate portion of the spadix falls free at this time as well and the berries are exposed on the remaining pistillate portion of the spadix (Fig. 33, *Philodendron hebetatum*). In the process of unfolding, the spathe often develops deep longitudinal fissures, which apparently enable it to unfold. Sometimes the old persistent spathe persists on the peduncle with fragments of the inner surface exposed (Figs. 35, 36).

The berries of *Philodendron* are cylindrical to obovoid, generally with a thickened cap-like apex and not markedly colored, though berry colors from pale yellow to bright orange or even red to purple

do exist (see section on berry color). Berries in *P.* subg. *Philodendron* are universally soft and fleshy except for the frequently thickened apex. The seeds can be seen easily through the sides of the berries. When fully mature the apical portion of the berry is easily torn free, and the thin, fragile sides of the berries are easily ruptured (see section on seeds).

Though little is known about fruit dispersal, the mesocarp surrounding the seeds contained within each locule is juicy or gelatinous and is usually sweet and sticky, making it logically animal dispersed. Infructescences that appear to have been pecked apart by birds (Fig. 36) are frequently seen. Certainly the sticky seeds, often many per berry, would logically be easily dispersed on birds' beaks. Alternatively, the infructescence is large, and even faintly scented when fully mature, making it an appealing meal even for mammals such as monkeys. Grayum (1996) theorized that those species of *P.* subg. *Pteromischum* with whitish fruits, which may produce a garlic-like or pepper-like odor at night, are dispersed by bats. Those with orange fruits may be dispersed by diurnal animals. Certainly the manner in which many species of *P.* subg. *Pteromischum* flower, e.g., on the ends of short, spreading branches some meters above the ground, would make them superbly positioned as bat fruits. There are also species of *P.* subg. *Philodendron*, such as *P. lentii*, which have their branches held in a similar manner.

Ants are also probable dispersers of *Philodendron* seeds. I have seen two different species of ants carrying away individual seeds of *Philodendron*. Ant dispersal is certainly important for those species, such as *P. megalophyllum* in South America, that live almost exclusively on ant nests. One cultivated individual of that species even set fruit repeatedly without being pollinated. Doing so in nature would provide a steady, abundant supply of berries for its ant dispersers and assure the species widespread dispersal. Indeed, the species is particularly successful even in areas of white sand soil where soil nutrients are very low.

Although berry color is known for only a relatively small number of *Philodendron* species (53 out of 96), some general comments can be made. Berry color in *Philodendron* is not so important taxonomically as it appears to be in *Anthurium* (Croat, 1983a, 1986a, 1991). Grayum (1996) reported that for *P.* subg. *Pteromischum* the fruits sometimes provided taxonomically significant characters, with species related to *P. inequilaterum* having orange fruits while other species have whitish fruits.

Mature berries of most *Philodendron* species are generally described as "white," but are usually more nearly ochraceous or somewhat greenish white. A total of 33 species have either white, creamy white, or greenish white fruits at least some of the time. In some species, such as *P. advena* and *P. smithii*, the whitish berries turn somewhat yellowish when fully mature, and the mature fruits of *P. brevispathum* are pale yellow. The berries of *P. sagittifolium* are usually pale yellowish but rarely have been reported as orange. While the majority of *Philodendron* berries are whitish, 17 species of Central American *P.* subg. *Philodendron* are known to have berries at least sometimes pale orange to orange. An additional three species have yellow or yellowish berries. *Philodendron fragrantissimum* has bright red to purple-red berries.

Known species with orange fruits are members of *P.* subsect. *Glossophyllum*. These are: *P. auriculatum*, *P. bakeri*, *P. cotonense*, *P. pseudauriculatum*, *P. wendlandii*, and *P. wilburii*. Other species with orange fruits are *P. anisotomum*, *P. brenesii*, *P. crassispathum*, *P. ferrugineum*, *P. lentii*, as well as, at least sometimes, *P. jacquinii* and *P. sagittifolium*. Three of the above, *P. brenesii*, *P. crassispathum*, and *P. lentii*, are members of *P.* ser. *Ecordata*. Thus, it may be significant that most species with decidedly orange fruits are members of *P.* sect. *Calostigma*. Even *P. ferrugineum*, with orange berries, and *P. sagittifolium*, sometimes with orange berries, are members of *P.* sect. *Calostigma*. Only *P. anisotomum* (*P.* sect. *Tritomophyllum*) and *P. jacquinii* (*P.* sect. *Macrogynium*) are not members of *P.* sect. *Calostigma*.

The seeds of *P.* subg. *Philodendron* are few to many per berry and are mostly oblong to oblong-ellipsoid, ellipsoid, ovoid-oblong, or less frequently ovoid. Typically they are minute (see below). The seeds are typically more or less terete, though they may be somewhat flattened, e.g., in *P. findens*. They have a rather thick, smooth (e.g., *P. granulare*) or striate-costate testa, as well as copious endosperm. The longitudinally oriented striations may be weak (*P. advena*, *P. findens*, *P. cotonense*, *P. purpureoviride*, and *P. sagittifolium*) to strong (*P. ferrugineum* and *P. grandipes*). Seeds of *Philodendron microstictum* have both longitudinal striations and much finer cross-etching. A number of species are reported to have seeds with pale raphide cells on the surface. These include *P. hederaceum* and *P. warszewiczii*. Seeds of some species, e.g., *P. anisotomum* and *P. hederaceum*, sometimes have a constriction on the end opposite the funicule.

Philodendron seeds are usually dramatically smaller than those of *Anthurium*, which typically have only two seeds per berry. Seeds of species of *P.* subg. *Philodendron* studied (a total of 48 species)

ranged from 0.5 mm to 5 mm and averaged 1.67 mm long; seed diameter ranged from 0.1 to 3 mm, averaging 0.7 mm. The longest seeds were those of *P. jacquinii* and *P. hederaceum*, at 5 mm. Relatively few species have seeds longer than 2 mm: *P. advena*, *P. anisotomum*, *P. findens*, *P. dolichophyllum*, *P. grayumii*, *P. purulhense*, *P. rothschuhianum*, *P. sagittifolium*, and *P. warszewiczii*.

The number of seeds in each locule is often many fewer than the average number of ovules per locule, presumably owing to the fact that not all are properly pollinated. A careful examination sometimes shows the aborted undeveloped ovules that were present at the time of flowering. The percentage of ovules in each locule that develops into seeds varies from species to species. Species of *P.* sect. *Calostigma* that have only one or a few ovules per locule are more likely to have an equal number of seeds. On the other hand, species in *P.* sect. *Philodendron*, especially those with large numbers of ovules per locule, rarely develop all their ovules.

Because species of *P.* sect. *Calostigma* have fewer ovules per locule and thus fewer seeds, one might expect them to have larger seeds. Though admittedly the sample size was small (only 21 species studied for *P.* sect. *Calostigma* and 17 for *P.* sect. *Philodendron*), the unexpected results were that the seeds of species of *P.* sect. *Philodendron* in Central America averaged slightly larger than those of *P.* sect. *Calostigma* (to 1.69 mm long for *P.* sect. *Philodendron* and to 1.66 for *P.* sect. *Calostigma*).

Philodendron seeds are largely pale in color, mostly shades of brown, tan, or white, though for most species mature seeds have not been observed. Seeds vary in color from medium green (*P. rothschuhianum*) to whitish (*P. roseospathum*), tan (*P. alticola*, *P. annulatum*, *P. granulare*, *P. morii*, *P. smithii*), yellowish or pale yellow (*P. brenesii*, *P. llanense*, and *P. strictum*), yellow-orange (*P. crassispathum*, *P. purpureoviride*, *P. wilburii*, and *P. mexicanum*), brown (*P. ferrugineum*), or reddish brown (*P. heleniae*). The dried seeds of two species, *P. findens* and *P. jefense*, are described as translucent.

Pollination Biology

Although there are frequent insect visitors to *Philodendron*, especially small Hemiptera in the genus *Neelia*, which appear not to feed or mate on the inflorescences (H. Young, pers. comm.), only the larger beetles are known to be pollinators. The system of pollination is nearly identical to that of *Dieffenbachia* (Croat, 1983b; Young, 1986, 1990). Pollinators are members of subfamily Dynastinae in the family Scarabaeidae (Fig. 32). All determined beetles collected from either Central American or South American *Philodendron* are members of the genera *Cyclocephala* and *Erioscelis*. Some species of beetles are not particularly host-specific, visiting members of both *P.* subg. *Philodendron* and *P.* subg. *Pteromischum*; other genera such as *Dieffenbachia*, *Homalomena*, *Syngonium*, and *Xanthosoma*; and sometimes even other families including some palms (Arecaceae), *Cyclanthus bipartitus* Poit. ex A. Rich (Cyclanthaceae), as well as *Annona* and *Cymbopetalum* in the Annonaceae (M. Grayum, pers. comm.; Schatz, 1990). *Cyclocephala negerrima* Bates, for example, has been found visiting *P. brenesii* and *P. tysonii*, but also *P. standleyi* Grayum, a member of *P.* subg. *Pteromischum* (see Table 3). Though beetles are not very species-specific pollinators, individual beetles of some species tend to be somewhat stratum-specific, visiting only those species growing at particular height ranges above the ground (Schatz, 1990; Helen Young, pers. comm.). These beetles are attracted to the *Philodendron* inflorescence, usually late in the day or at dusk. Attractants and/or rewards are apparently a combination of scent (at least in many cases), a source of food (oil-bearing sterile staminate flowers), warmth (thermogenesis), and shelter.

Scents produced by *Philodendron* species are not always obvious, at least in *P.* subg. *Philodendron*. George Schatz and Helen Young (pers. comm.) have documented floral odors for species of *Philodendron* and have identified the principal constituents of these aromas. Some species have noticeably sweet aromas in the early evening hours, while other species have no noticeable scent, at least during the early evening hours on the first day of anthesis. *Philodendron megalophyllum* (in cultivation at the Missouri Botanical Garden), a South American species, had a faint spicy aroma detectable directly at the spathe during the evening, but even this faint aroma was absent the following morning on day two of the flowering event. At the same time the stigmas were soft, juicy, and sticky but without an obvious flavor or taste both in the evening and the following morning. Schatz (1990) believed that the pattern of visitation to *Philodendron* exhibited by beetles at La Selva in Costa Rica was to a great degree explained by odor. He pointed, for example, to the high degree of specificity exhibited by *Philodendron radiatum* and an undescribed species of *Cyclocephala*. The aroma given off by *P. radiatum* was made up of compounds unique to that species.

At anthesis the open spathe of *Philodendron* provides ample space at the base in the area surrounding the pistillate portion of the spadix. The spathe

blade may provide a certain amount of protection against rain, as mentioned previously. Beetles typically spend the first night and most of the following day inside the spathe where they remove the sticky exudate from the pistils, eat pollen (Gottsberger & Silberbauer-Gottsberger, 1991), feed on the sterile staminate flowers, and mate. Studying *P. bipinnatifidum*, Gottsberger and Silberbauer-Gottsberger (1991) found that the beetles were active mostly during the first 10 to 20 minutes after arrival and during the strongest production of scent. Copulation was most active immediately after arrival, when the spadix was warmest; grazing on the sterile male flowers also subsided by the time the spadix had cooled off. Old inflorescences that have been pollinated often have the sterile staminate portion of the spadix entirely eaten away.

Typically the number of beetles found in a single inflorescence is modest, frequently no more than five and sometimes up to a dozen beetles. However, sometimes the numbers are simply astounding, with Gottsberger and Amaral (1984) reporting as many as 200 beetles in a single inflorescence of *P. bipinnatifidum*. While visiting beetles are often of the same species, sometimes more than one species of beetle may be found in the inflorescence. Though beetles typically do not leave the spathe until about dusk, they will leave if the inflorescence is sufficiently disturbed. When beetles are disturbed, they may crawl slowly up the spathe or spadix and appear at the rim of the open spathe, at which point they generally fall promptly to the ground where they disappear in the leaf litter or soil with remarkable speed.

Thermogenesis, the production of heat in the spadix by the rapid oxidation of stored starch or lipids (Walker et al., 1983; Gottsberger, 1990), plays an important role in the pollination of *Philodendron* (van Herk, 1937a–c; Van der Pijl, 1937; Knutsen, 1974; Seymour et al., 1984). Gottsberger (1984, 1986), studying *P. bipinnatifidum*, has shown that, although oxidation of carbohydrates takes place during preheating of the spadix, lipids are oxidized thereafter during maximum heating and are consumed directly, not after conversion to carbohydrates. This makes the biochemistry of this species similar to that accompanying heat production in some animals. The thermogenic reaction occurs principally in the staminodial region of the staminate portion of the spadix (James & Beevers, 1950; Henry & Nyns, 1975) involving the inner surface of mitochondrial membranes (Urdentlich et al., 1991) and is triggered by an accumulation of salicylic acid (Meeuse & Buggeln, 1969; Raskin et al., 1987, 1989; Meeuse, 1975, 1978; Raskin, 1992). The end result of this high rate of respiration in these plants is the production of heat rather than ATP as in animals (Meeuse, 1966). To accomplish this high increase in metabolism the plant's mitochondria in the inflorescence switch to an electron transport pathway commonly referred to as the "cyanide-resistant pathway."

The thermogenetic heat rise in *Philodendron* is sometimes dramatic, with temperatures rising well above ambient temperature (Nagy et. al., 1972; Knutsen, 1974). Gottsberger and Silberbauer-Gottsberger (1991), working with *P. bipinnatifidum*, reported temperatures of spadices occasionally to 46°C with the highest and most efficient temperatures for the emission of scents being maintained for 20–40 minutes. Thermogenesis does not create even or constant temperatures, but rather produces fluctuations depending on the time of day with definite peaks (Leick, 1910, 1916; Engler, 1920a, 1920b; Foster, 1949; Nagy et al., 1972; Sheridan, 1960; Gottsberger & Amaral, 1984), the greatest occurring when beetle visitation and odor is most intense (Gottsberger & Amaral, 1984). Temperature peaks may occur on two or more successive days. While the increased temperature is presumably responsible for the production of scent compounds (Nagy et al., 1972), and whereas the production of heat and scent appears closely correlated with peaks in temperature, there is still controversy over the exact function of the heat production at least as it pertains to genera that produce foul odors. Moodie (1976) suggested that heat production and the higher levels of carbon dioxide production are components of a carrion, dung, and mammal mimicry syndrome and that heat production aids in providing sufficient warmth in colder climates for the activity of pollinating organisms. The subject of thermogenesis and its role in pollination has been reviewed in great detail by Mayo (1986), Grayum (1990), and Bay (1995[1996]).

The exact role that thermogenesis plays in the pollination of *Philodendron* is still poorly known, and rather few plants have been studied on an experimental basis. Despite its probable occurrence in all *Philodendron* species, thermogenesis has thus been documented only for *P. selloum* K. Koch and *P. bipinnatifidum*, now considered by Mayo (1991) to be synonymous. My own measurements with a recording thermometer on *P. glanduliferum* and *P. advena* in the field in Chiapas, Mexico, indicated a definite heating during the early evening hours, usually peaking between 18:00 and 19:00 hours.

The site of the heat production on the spadix is another possible difference between *P.* subg. *Meconostigma* and *P.* subg. *Philodendron*. Mayo's

(1986) investigations on *P.* subg. *Meconostigma* indicated that heat production was centered in the sterile staminate section of the spadix. In *P.* subg. *Meconostigma*, that section is as large as or larger than the fertile staminate part of the spadix, a situation unknown in *P.* subg. *Philodendron* where the staminodial segment is always a small percentage of the total spadix.

Contrary to Mayo, Leick (1916) reported that heating took place in the "middle and upper part" of the spadix in *P. selloum*, presumably implying at least a part of the fertile staminate portion. Concurring with this view, Ron Weeks (pers. comm.) reported that a perceived temperature rise occurred in both the sterile and fertile staminate spadix portions of those species of *P.* subg. *Meconostigma* that he studied. Mayo (1986) theorized that, because of the major morphological differences in the relative lengths of the sterile and fertile staminate portions of the spadices, the two subgenera would likely have different thermogenetic patterns.

In the Central American *Philodendron* species observed by the author, the spathe opens broadly late in the afternoon of the first day of flowering; it closes slightly the morning after the first night of anthesis. The evolutionary significance of this slight closure is uncertain but, even in the most extreme cases, it occludes only the pistillate portion. The spathe continues to close on the evening of the second day after having been open for about 24 hours (see discussion below). The beetles, which generally enter the spathe on the first night of opening, spend about 24 hours in the spathe tube. This second partial closing process usually corresponds with staminal dehiscence. The now crowded condition of the spathe tube, and the probable desire on the part of the beetles to seek a new food source with the onset of dusk, encourages the beetles to leave the inflorescence. The beetles emerge from the spathe tube by either climbing up the side of the spadix or up the inside wall of the spathe. By the time they emerge from the spathe, it is quite constricted and they must squeeze through the constriction which fits rather tightly around the spadix just above the sterile staminate portion. In order to depart the beetles must literally crawl through the copious strands of pollen that emerge from the apical pores of the stamens. The constriction of the spathe and its corresponding constricted area on the spadix help to insure that most of the pollen that falls into the spathe tube accumulates and is carried forward and out of the spathe by the departing beetles. Araceae pollen is not very tacky and probably does not adhere well to the smooth, hard surfaces of the beetles. However, the beetles themselves are usually quite sticky from the sugary secretions of the styles and especially from the resin, which arises usually from the inner surface of the spathe or sometimes from the spadix itself (Fig. 128). Once the beetles have emerged they fly off in search of another place to spend the night, usually another open inflorescence. The beetles apparently have a keen perception of infra-red radiation or of scent because they are often seen in a "homing-in" pattern, which is quite direct to the next available inflorescence (John Rawlins, pers. comm.). Gottsberger and Silberbauer-Gottsberger (1991) reported that beetles flew in a zig-zag pattern toward the center of fragrance concentration, indicating that they were very sensitive to the aroma being produced. They also reported that once the beetles were within sight of the inflorescence they shifted to a straight line of flight until they hit the inner surface of the spathe blade, whence they moved into the lower portion of the spathe. Gottsberger and Silberbauer-Gottsberger (1991) have proven experimentally in the case of *P. bipinnatifidum* (a member of *P.* subg. *Meconostigma*) that the beetles use only visual references for location as they near the inflorescence. Shelter, warmth, food, and copulation are the driving forces behind this pollination strategy, and although selectivity is not perfect in such beetle-pollinated systems (Young, 1986, 1988a) fruit-set in undisturbed populations is high. The precision and high degree of synchrony of thermogenesis gives evidence of a highly evolved system of pollination.

Even though all detailed observations thus far have been made with *P. bipinnatifidum*, there is considerable confusion regarding the results. Horticulturist Ron Weeks (Homestead, Florida) reported (pers. comm.) that three members of *P.* subg. *Philodendron*, *P. bipinnatifidum*, *P. speciosum* Schott, and *P. williamsii* Hook. f., showed no variation in the schedule of spathe opening, the capability of the plants being hand-pollinated on the first evening of opening, or in the shedding of pollen on the evening of the second day. On the other hand, he reported that *P. eichleri* Engl. showed great variation in opening periods, temperature changes, fragrance, and pollen shed, perhaps owing to weather conditions. Scientific studies carried out on other plants in *P.* subg. *Meconostigma* showed considerable variability. Four separate and conflicting reports were made on material determined as belonging to *P. bipinnatifidum* in Brazil. Warming (1867, 1883) reported a two-day pollination event with two heat peaks (early evening and late morning, respectively) with the spathe closing then reopening during the first night. Gottsberger and

Amaral (1984) reported on two plants, one as *P. selloum* (now considered to be a synonym of *P. bipinnatifidum*) with a three-day pollination event with two unequal early evening heat peaks, and one as *P. bipinnatifidum* with a four-day pollination event with three unequal early-evening heat peaks. The spathe was not reported to close during the event. Confirming the complexity of the thermogenesis riddle is the fact that Seymour et al. (1983), studying a cultivated but similar plant believed to be the same species (Mayo, 1986), found both types of pollination events that had previously been described by Gottsberger and Amaral but this time in a single plant. Clearly more investigation must take place, at least in *P.* subg. *Meconostigma*, to determine the pollination behavior.

Leick (1916), reviewing work done by Kraus (1894, 1896) with *P. bipinnatifidum*, a member of *P.* subg. *Philodendron* from Venezuela, reported a two-day pollination event with temperature peaks in the evening of two consecutive days. While it is not certain that most Central American *Philodendron* have an elevated temperature on two consecutive days, the general pattern of opening and closing of the spathe and the beetle visitation in *P. bipinnatifidum* would appear to match the events of Central American species observed in the field and under greenhouse conditions at the Missouri Botanical Garden. Further detailed studies of this phenomenon, including a much broader survey of Central American species, will be carried out by my student, Jane Whitehill, during graduate studies at the Missouri Botanical Garden.

Grayum's (1996) observations with *Philodendron* subg. *Pteromischum* showed a similar pattern, with most species having the spathe beginning to loosen by early afternoon and being fully open by mid-afternoon. He reported that for the species of *P.* subg. *Pteromischum* he observed, the pollinators appeared at the opened inflorescence during a relatively brief time, usually between 19:00 and 19:15 hours. An important feature in the pollination story reported by Grayum (1996) for the first time is that resin secretion from the inner spathe surface does not begin until 21:00 to 22:00 hours on the first day of anthesis, and that it then continues until the end of anthesis.

Once opened, the spathes of *P.* subg. *Philodendron* apparently remained open during the night and were always open the next morning at the beginning of day two, remaining open during the course of most of the day. During the latter part of the same day, usually in late afternoon of day two, the spathe began to close and pollen began to shed in long filaments. The spathe did not fully close at this time but remained open near the apex. It remained in this condition into the beginning of the evening of day two. By the beginning of day three the spathe was generally fully closed, and the only evidence that it had ever opened was often some loose pollen remaining on the closed edges of the spathe. In addition, the closed spathe is somewhat less turgid than before anthesis, sometimes allowing it to be forced open without breaking the margins of the spathe. Doing the same with an unopened spathe is impossible without breaking the stiff and brittle spathe margins.

The entire pollination episode usually requires little more than 24 hours, counting just the time that the beetles are present. The time that the spathe is to any extent open could be as much as 8 hours longer, since it may open late in the afternoon and remain open for some hours after the pollen has been shed. Grayum (1996) reported that for the species of *P.* subg. *Pteromischum* studied in Costa Rica the average pollination event required about 30 hours (i.e., from spathe opening to closing).

That the intensity of light must play an important role in flowering behavior is indicated by the fact that on cloudy days spathes in cultivated collections open earlier than usual, sometimes as early as noon on day one of the flowering sequence. This may support the argument of Buggeln et al. (1971) that darkness induces opening of the spathe and an elevated respiration rate in *Sauromatum venosum* Kunth.

Armbruster (1984), studying the role of resin in angiosperm pollination, has questioned the efficacy of floral resin in the transport of pollen, citing its possible toxicity and the difficulty of transporting pollen embedded in resin. While he stressed the role of resin for other purposes, mainly in nest-building by bees, it must be pointed out that bees which use resin for nest building play no role whatever in *Philodendron* pollination. In contrast, the general availability of resin, its close association with pollen delivery, the non-tacky nature of *Philodendron* pollen, and the availability of resin only at anthesis all point to a strong role for resin in *Philodendron* pollination. In species with resiniferous spadices (Fig. 128), the pollen is shed with and incorporated in the resin from the moment of theca dehiscence. Alternatively, species that lack staminal resin and instead have resin only on the inner spathe surface have pollen presented as slender filaments.

Breeding studies (see section on Breeding Behavior) have shown that *Philodendron* species have few if any genetic barriers to cross-pollination, ow-

ing perhaps to the fact that there are other physical and temporal barriers to self-pollination. Even when two species of *Philodendron* are in flower simultaneously, there are other parameters that effect separation. Beetles tend to fly at certain elevations above the ground (Schatz, 1990), helping to prevent cross-pollination of species that flower at different strata. In addition, specific attractants, i.e., species-specific pheromones, may exist in some species that attract principally a single beetle species (H. Young, pers. comm.). The sloppiness in the system, when it occurs, is owing to opportunistic beetle visitors (G. Schatz & H. Young, pers. comm.), and this might produce some hybridization.

Perhaps because of the substantial barriers already present, *Philodendron* appears to have developed the ability to cross between sections. In *Anthurium*, relatively little cross-breeding was possible between different sections in the genus (Croat, 1991). In contrast, quite unrelated species of *Philodendron*, even species in different sections, readily cross-pollinate and produce intermediate offspring (Keith Henderson, Cairns, Queensland, Australia, pers. comm.). For this reason pre-zygotic separation may be critical to maintaining distinct species lines. The pollinators of *Philodendron*, dynastine scarab beetles, are for the most part not very species-specific and frequently switch from one species to any other in flower at the same time. Not only will some species of beetles switch from one *Philodendron* species to the next, as is known for certain in *Dieffenbachia* (Young, 1986), but some individuals will also switch to another genus. For example, beetles that regularly visit *D. longispatha* Engl. & K. Krause at La Selva may visit *P. grandipes*, another species that is terrestrial and about the same height above the ground (G. Schatz & H. Young, pers. comm.). Beetles are also reported to move from *Dieffenbachia longispatha* to *Xanthosoma undipes* (K. Koch & Bouché) K. Koch. Some individuals of beetle species that regularly visit *D. longispatha* will even switch to *Cyclanthus bipartitus* Poit. (Cyclanthaceae). Schatz believes that this is owing to the fact a small component of the pheromone emitted by *Cyclanthus* Poit. ex A. Rich is the principal component of the scent given off by *Dieffenbachia longispatha*. He believes that during the end of the flowering season of *Dieffenbachia* and the beginning of the flowering season of *Cyclanthus* some confusion occurs in the pollinators' behavior.

The unpublished observations of G. Schatz and H. Young (pers. comm.), and the published results reported by Helen Young (1986, 1988a, 1988b) principally for *Dieffenbachia*, probably are comparable to what is happening in *Philodendron*. Beetles that visit any particular species of *Dieffenbachia* are often predominantly of one species, but they are often accompanied by other opportunistic beetles. Schatz believes that these opportunistic species are not likely to be effective pollinators, since they are so catholic in their tastes that they are not likely to make their next visit to a receptive *Dieffenbachia*. Likewise, Helen Young (Young, 1988a) indicated that the most common species of beetles are not the most effective pollinators. However, they may be responsible for the occasional hybrids seen in *Dieffenbachia*, at La Selva, where the studies of both Schatz and Young were carried out. The pollination system described for *Dieffenbachia* by Young and Schatz is apparently similar to that of *Philodendron*. Schatz (pers. comm.) reported that while one undescribed beetle species (determined as *Cyclocephala ampliata* by H. Young), was found to visit only *Philodendron radiatum*, it was accompanied occasionally by another more opportunistic species. Despite the presence of opportunistic beetle species, some beetle pollinators of *Philodendron* species are probably much more species-specific. For example, Grayum (1996), citing unpublished data collected by George Schatz, reported that two unrelated species of *Philodendron* subg. *Pteromischum* were pollinated by the same species of beetles, and that both *Philodendron* species have floral odors featuring the same two principal components. This leads to the conclusion that there is a degree of specificity among pollinators for certain species based on their floral odors. In addition, in the list of pollinators known for *P.* subg. *Philodendron* (see Table 3), only three *Philodendron* species were observed to have more than a single species of beetle present at any one time. In each case, two species of beetles were present. As can be seen from *P. grandipes* (Table 3), the beetle species need not always be the same. Though more studies must be made on pollination biology of *Philodendron*, and even though the beetle pollination system is somewhat sloppy and imprecise, a combination of a moderately strong beetle-plant specificity, coupled with severe phenological constraints and narrow windows of pollination opportunities (perhaps as little as a few hours per year), works to reduce interspecific hybridization. Although hybrids can be readily produced under greenhouse conditions, evidence for hybridization is not usually apparent among wild populations.

BREEDING BEHAVIOR

In comparison to *Anthurium*, where breeding studies were easy to conduct (Croat, 1980, 1983a,

1986a, 1991), *Philodendron* pollination was difficult. Cross-pollination attempts were easy in *Anthurium* owing to their hermaphroditic flowers and because plants often had several inflorescences per plant in different stages of development. In addition, the plants reached anthesis during the day when greenhouse personnel and volunteers were available to make cross-pollinations. In *Philodendron*, the number of inflorescences available was always fewer than in *Anthurium*; *Philodendron* sometimes produced only a single inflorescence per season. In addition, *Philodendron* was very seasonal in its flowering behavior (unlike *Anthurium*, which sometimes flowered all year), making pollination all the more difficult. When flowering did occur it was often unexpected since it is difficult to tell when the spathe is ready to open. Moreover, the spathe generally opens for one day only. Opening usually took place late in the afternoon after greenhouse personnel left. Even if the opening inflorescence was found in time, it was generally impossible to find another plant with fresh pollen to use for purposes of experimental crosses. *Philodendron* pollen does not remain viable very long, though it can be kept viable for a time in glassine envelopes. Ron Weeks, a grower from Homestead, Florida, reports (pers. comm.), that he stores pollen in film canisters at refrigerator temperatures and that it remains viable for several weeks. He also reports that inflorescences cannot be pollinated after the first evening they open. After the spathe opens (generally late in the day) it is only during the evening and night of the first night that the pistillate flowers are believed to be receptive. Attempts to pollinate plants with their own pollen have always failed if one waits until the pollen emerges. It should be noted, however, that Grayum (1996) reported that, based on the use of peridoxase paper, which purportedly indicates the receptivity of stigmas (Young, 1986), the stigmas were receptive for up to 24 hours after anthesis. Though it seems unlikely that pistillate flowers are receptive after the first evening of anthesis, the pistillate flowers are receptive for an unknown period of time before the spathe opens, so that most successful pollinations usually involved cutting a hole in the spathe after obtaining very fresh pollen from a plant in the staminate phase of flowering. Though one can completely remove the spathe then protect the developing pistils with a plastic bag, it is better to simply cut a window in the spathe large enough to see most of the spathe. Then with a small brush one can spread pollen over as many of the pistils as possible, again covering the spathe for a time with a plastic bag to insure that the pollen does not dry out and fail to germinate. An effective means of spreading the pollen to insure adequate and uniform coverage is to mix the pollen with water.

Failure to remove or at least loosen the bag used to cover the pollinated spadix later may result in mold developing in the spathe. Unpollinated inflorescences usually fall off within a week or two. Ron Weeks (pers. comm.) reported that for *P.* subg. *Meconostigma* in Florida the unpollinated inflorescences may persist for up to a month. Development time for fruits ranges from only a few weeks or more generally a few months and sometimes nearly a whole year. Ron Weeks (pers. comm.) reports that in *P.* subg. *Meconostigma* fruits ripen in South Florida in 2.5 to 3 months.

Phenology

Based on a field-oriented study of phenology and pollination behavior carried out at La Selva in Heredia Province, Costa Rica, Grayum (1996) reported species of *P.* subg. *Pteromischum* flowered for periods of 4–8 weeks. Obviously, since most members of *P.* subg. *Pteromischum* have only one or two inflorescences per axil, vs. sometimes 4 or more for *P.* subg. *Philodendron*, the flowering episodes of the latter might be longer than two months. The flowering events, however short or long, are not necessarily the same year after year. I suspect that, like understory vegetation (Croat, 1975), their flowering phenology may be affected by the onset of the rainy season.

Based primarily on a phenological survey of herbarium collections, flowering (and to a lesser extent fruiting) behavior has been studied here for Central American species of *P.* subg. *Philodendron*. These studies resulted in a phenological statement for each species. This statement follows the description of each species as a part of the discussion. Some general comments regarding phenology are important.

In studying herbarium material for phenological variation it is often difficult to determine the exact state of the inflorescence. However, with experience it is relatively easy to distinguish inflorescences that have never opened, i.e., pre-anthesis, from those which have already opened. Spathes that have never opened are very tightly closed, whereas those that have already undergone anthesis are not so tightly closed. By dissecting the spathe one can quickly determine if the pollen has emerged. If so, the spathe has already opened and reclosed over the spadix.

Spadices at anthesis when they are collected are usually easy to discern as well because they are

typically opened when pressed. It is difficult, however, to easily predict the age of an inflorescence beyond anthesis and before swelling due to the enlargement of the pistils. Since an inflorescence at anthesis is rare (open less than 24 hours), while every successfully pollinated inflorescence persists for one to many months, there will always be many more collections with "post-anthesis" inflorecences than those described as "in flower."

Central American members of *P.* subg. *Philodendron* fall into several phenological groups. All of these categories can have variations, and flowering is rarely consistent throughout any period. Some categorizations are tentative, as listed in Appendix 4, "Phenological Patterns of Central American *Philodendron* subg. *Philodendron*."

The flowering patterns of Central American members of *P.* subg. *Philodendron* are as follows:

A. FLOWERING IN DRY SEASON AND WET SEASON

This is the largest flowering category among Central American *P.* subg. *Philodendron.* A total of 47 species fall into this category, including *P. fragrantissimum, P. panamense, P. sagittifolium, P. grandipes, P. pterotum,* and *P. radiatum.* Although these species begin flowering during the dry season, the dry season rarely constitutes the period of greatest flowering activity (except perhaps in the case of *P. hederaceum,* a species which though apparently flowering all year and thus aseasonal appears to have more flowering collections made during the dry season than at any other time of the year). Low flowering activity is particularly characteristic of species inhabiting regions of *Tropical moist forest* or other areas where marked seasonal changes are apparent and affect the availability of beetle pollinators.

Those species occurring in cloud forest habitats (usually *Premontane rain forest* or *Lower montane wet forest*) also seem to have more flowering in the rainy season even though they are more apt to be in flower in the dry season than their *Tropical moist forest* counterparts.

Though perhaps it is merely a matter of poor sampling, species more common, widespread, or locally abundant tend to have flowering seasons that extend from the dry season to the wet season, whereas rare species seem much more likely to have flowering restricted to either the dry or the wet season.

B. FLOWERING ONLY IN WET SEASON

This is the second largest flowering category, comprising 30 species (32 taxa) believed to flower exclusively in the wet season (roughly between May and December in Central America). They represent largely rare or narrowly distributed species for the most part and are often species that inhabit the wettest and frequently the coolest forest types such as *Tropical wet forest, Premontane wet forest, Premontane rain forest,* and *Lower montane wet forest.* Examples of species in this flowering type are: *P. albisuccus, P. antonioanum, P. chiriquense, P. coloradense, P. correae, P. cotobrusense, P. dominicalense, P. dodsonii, P. ferrugineum, P. gigas, P. hammelii, P. jefense, P. madronense, P. niqueanum, P. pirrense, P. purulhense, P. squamicaule,* and *P. ubigantupense.*

Not all species that flower exclusively in the wet season occur in very wet or cool forest. A few species flower only in the wet season because the dry season in the region where they occur is often too severe, perhaps so severe as to limit the beetle pollinators. These include several Mexican species, e.g., *P. basii, P. breedlovei, P. dressleri,* and *P. sousae.*

C. FLOWERING ONLY IN DRY SEASON

One of the most unusual flowering categories, and a relatively small one with only 7 species, is a group believed to flower only during the dry season (January to April in Central America). This group is diverse and difficult to characterize. Some of the species, such as *P. bakeri, P. brewsterense, P. chiripoense, P. edenudatum, P. folsomii,* and *P. knappiae,* occur in wet to very wet areas, some in areas where weather conditions are so bad in general during the rainy season that it may be more efficient to compete for pollinators during the dry season (which would not be very dry in any event). *Philodendron dwyeri* is unusual in that it flowered at the beginning of the dry season in an area that in general is quite arid in this season. It is known from only a single individual and may have represented an unusual, out-of-phase flowering.

D. FLOWERING ALL YEAR

Species that flower aseasonally are usually common species such as *P. hederaceum* (though it apparently flowers more frequently in the dry season) and *P. jacquinii* (which is also often edaphically versatile or less subject to the pressures of the environment). Though not as widespread as the two aformentioned species, *P. advena,* another member of this group, is a tough, highly variable and ecologically adaptive species. *Philodendron purpureoviride* has much the same edaphic preferences as *P. hederaceum,* although it is much less widespread.

Both are highly adaptable, scandent species. *Philodendron hederaceum*, though flowering all year, is even more commonly in flower in the dry season than in the wet season. *Philodendron radiatum*, also a member of this group, is as widespread and even more common than *P. hederaceum*.

E. FLOWERING BIMODALLY

Based on the historical record of herbarium collections, only a few species are expected to flower twice per year. This pattern may be much more common and simply masked by the year-to-year variation in flowering behavior. Grayum (1996) reported bimodal flowering to be common with *P.* subg. *Pteromischum*. He indicated that the two modes were quite unequal, that one of them involved far fewer individuals and lasted for a shorter period of time. Among species of *P.* subg. *Philodendron*, *P. aromaticum* appears to flower in the mid-dry season and mid-wet season. It is possible this species is just too poorly known to determine its phenology. *Philodendron morii* may also flower bimodally, with flowering collections seen in March and November, and with immature fruiting collections in December, February, and June. *Philodendron wilburii* appears to flower at the beginning of the dry season and primarily later at the beginning of the rainy season.

Several species are poorly known phenologically because of sparsity of flowering collections: e.g., *P. dominicalense*, *P. niqueanum*, and *P. ubigantupense* (all seen in flower only once during the early rainy season). All of these are assumed to be species that flower entirely during the rainy season.

Fruiting phenology in *Philodendron* subg. *Philodendron* is too poorly known to report on here. Most species appear to develop fruits from between one and four months after the time of pollination, depending on the size of the infructescence, but too few mature fruting collections were observed to determine the phenological period. Fruit development time is affected by the size of the infructescence. Species with small spadices, such as *P. heleniae*, produce mature berries faster than species with larger spadices.

CYTOLOGY

No karyological studies were made for this revision, but Petersen (1989) reviewed all chromosomal literature and made new studies. The chromosomes of *P.* subg. *Philodendron* are small, with counts of $2n = 30$, 32, 34, and 36 (rarely 26 and 48). Petersen (1989) speculated that the base number for the genus is 18. Very few of the 29 species (other names were synonyms or hybrids) for which chromosome counts have been reported are members of the genus from Central America. Those Central American species for which chromosome counts have been reported are: *P. radiatum* $2n = 32$, *P. microstictum* (as *P. pittieri*) $2n = 34$, *P. verrucosum* $2n = 34$, and *P. hederaceum* (as *P. scandens*) $2n = 36$. *Philodendron wendlandii* was counted at $2n = 54$, but Petersen believed this to be either an error in counting or not a *Philodendron*.

GEOGRAPHICAL DISTRIBUTION AND ENDEMISM

The *Philodendron* subg. *Philodendron* flora in Central America is diverse but heavily concentrated in the southeastern part near South America. Despite this, relatively few Central American species actually enter South America. Most species that do enter the South American continent range along the Pacific slope into northwestern Colombia and Ecuador, with relatively few occurring east of the Andes and even fewer entering the Amazon basin.

As was shown for *Anthurium* (Croat, 1983a, 1986a, 1986b), species diversity of *P.* subg. *Philodendron* shows a general diminution from Mexico to Middle America, followed by a marked increase approaching South America (Appendix 3, "Sectional Classification of *Philodendron*"). Distribution of *Philodendron* in Central America is as follows: Mexico has 21 taxa, Guatemala 15, Belize 9, El Salvador 5, Honduras 13, Nicaragua 18, Costa Rica 48, and Panama 82. Thus species diversity is greatest in Costa Rica and Panama, with 46% and 79% of the total Central American species, respectively. Collectively the number of species in these two countries comprises 90% of the species total.

Fifty-three species (58 taxa) of *P.* subg. *Philodendron* (nearly 59% of the total) are endemic to Costa Rica and Panama. Endemism is particularly high in Panama, where 38 taxa (34 species) of 81 (47%) are endemic. In Costa Rica 7 of 47 taxa (46 species) (15%) are endemic. Costa Rican endemics are: *P. aromaticum*, *P. auriculatum*, *P. chirripoense*, *P. cotobrusense*, *P. dominicalense*, *P. microstictum*, and *P. wilburii* var. *wilburii*. Mexico has a higher rate of endemism, with 7 of 21 (20 species) (33%) endemic. Mexican endemics are: *P. basii*, *P. breedlovei*, *P. dressleri*, *P. radiatum* var. *pseudoradiatum*, *P. hederaceum* var. *oxycardium*, *P. sousae*, and *P. subincisum*. In Middle America little endemism occurs. With the exception of Belize, which has one endemic (*P. dwyeri*), no other country in Middle America has any endemic species.

The distribution of Central American *Philodendron* reflects the trend for endemism in the genus. Only 27 species (28 taxa) (a total of 26% of all Central American species of *P.* subg. *Philodendron*) range into South America, eight (7% of the total) only to Colombia (Appendix 1). These are: *P. heleniae*, *P. immixtum*, *P. ligulatum* var. *ligulatum*, *P. malesevichiae*, *P. mexicanum*, *P. pseudauriculatum*, *P. radiatum* var. *radiatum*, and *P. squamicaule*.

Sixteen Central American taxa occur in Ecuador (Appendix 1), all but two (*P. brevispathum* and *P. jacquinii*), ranging along the Pacific slope of the Andes. These are: *P. brunneicaule*, *P. dodsonii*, *P. grandipes*, *P. hebetatum*, *P. platypetiolatum*, *P. purpureoviride*, *P. hederaceum* var. *kirkbridei*, *P. hederaceum* var. *hederaceum*, *P. squamipetiolatum*, *P. scalarinerve*, *P. squamicaule*, *P. tenue*, *P. tripartitum*, and *P. verrucosum*. Of these 14 taxa, 1, *P. hederaceum* var. *kirkbridei*, skips Colombia or has not yet been collected there. *Philodendron dodsonii* is particularly unusual in being absent from Panama.

Eight Central American species, *P. brevispathum*, *P. fragrantissimum*, *P. hederaceum*, *P. jacquinii*, *P. jodavisianum*, *P. sagittifolium*, *P. strictum*, and *P. tenue*, range to Venezuela. The ranges of *P. brevispathum*, *P. fragrantissimum*, and *P. hederaceum* also extend into the Amazon drainage, while the others occur either on the northern slope of the coastal cordillera or otherwise in the drainage of the Orinoco River Basin. Curiously only four species, *P. brevispathum*, *P. fragrantissimum*, *P. hederaceum*, and *P. verrucosum*, occur in the Amazon drainage. Three additional species, *P. jacquinii*, *P. strictum*, and *P. tenue*, occur east of the Andes, but only along the Cordillera de Mérida, the Cordillera de la Costa or the northern part of the Guiana Highlands and within the drainage of the Río Orinoco.

The only truly widespread Central American species of *P.* subg. *Philodendron* is *P. hederaceum*, which occurs virtually throughout the Neotropics, and is one of only two species (the other being *P. verrucosum*) that occurs on both slopes of the Andes. *Philodendron fragrantissimum* is probably the next most widespread species, ranging from Belize to the West Indies and into South America to the Guianas, northern Brazil, and to southern Peru.

Further collecting in Colombia, especially along the western slope of the Andes, will probably change these statistics but the figures most likely reflect the realities of life zone ecology and geologic history of the area rather than under-collecting. Since relatively few species of Araceae are known to occur at lower elevations on both the eastern and western side of the Andes, it can probably be presumed that the evolution of the respective Amazonian and Pacific coastal floras occurred independently after the Andes began to arise toward the end of the Cretaceous (Raven & Axelrod, 1974). The relatively few truly wide-ranging species, i.e., those ranging from Mexico to Brazil, appear to attest to this isolation. In Central America only one species, *P. hederaceum*, really falls into such a category, and it is also common in the West Indies indicating that it may have an ancient origin (or be easily dispersed). The high rates of endemism in Costa Rica, Panama, and Mexico perhaps reflect the isolation of these areas during periods when the oceans were at much higher levels than they are today and when the area that is now central Panama and Costa Rica was disconnected from South America. Much of the present area of Central America was submerged during early times. At the close of the Tertiary, 800,000 years ago, sea level was about 100 m higher than today (Holmes, 1969). The land mass of what is now Central America began to emerge as a series of islands during the Oligocene with further uplifting during the Middle Miocene. It was not until the Upper Miocene and Pliocene that the final portions of the isthmus of Panama emerged above sea level (Torre, 1965), and the final connection of Central and South America was made about 5.7 million years ago. In order to place these geological events in relation to the modern aroid flora, it should be noted that even during this era precursors to the existing flora probably already existed, since the angiosperm floras of the Oligocene were believed to have consisted almost entirely of existing genera, and the floras of the Oligocene and Pliocene probably already had existing species (Takhtajan, 1969).

Just as important as geology, from the standpoint of the isolation of the Central American aroid flora, are ecological factors that would cause Central American species to be isolated from those of South America. Much of eastern Panama consists of broad expanses of *Tropical moist forest* with other, generally smaller areas of *Premontane wet* and *Tropical wet forest*. In contrast to Panama, much of the area of northwestern Colombia in the Department of Chocó consists of much wetter pluvial forest with annual precipitation often exceeding 11,700 mm in some parts of the region (Gentry, 1982). This broad band of pluvial forest with its own suite of unique endemic species no doubt acts as a barrier for species from regions with lesser rainfall amounts. It probably also accounts for the Panamanian and Costa Rican species that skip the wettest areas of northwest South America but recur in the relatively drier areas of mesic western Ecuador.

Just as the Central American *P.* subg. *Philodendron* flora is rather isolated from that of South America, there is a certain amount of isolation within different parts of Central America. In comparison to Mexico and Costa Rica/Panama, Middle America (Appendix 1) has low species diversity, with Guatemala having only 15 species, Honduras 13 species, and Nicaragua 18. Most of the species in Honduras, excepting *P. anisotomum*, *P. mexicanum*, and *P. warszewiczii*, are shared with Nicaragua (see Appendix 1). Nicaragua has eight additional taxa not shared with Honduras: *P. brevispathum*, *P. grandipes*, *P. immixtum*, *P. ligulatum* var. *ligulatum*, *P. platypetiolatum*, *P. pterotum*, *P. tenue*, and *P. wendlandii*. All of the latter are shared with Costa Rica and Panama. Guatemala shares only about half of its species with Honduras and Nicaragua, namely *P. fragrantissimum*, *P. jacquinii*, *P. jodavisianum*, *P. radiatum*, *P. sagittifolium*, *P. smithii*, and *P. tripartitum*. Its other species are shared only with Mexico (or rarely with Costa Rica and Panama, e.g., *P. mexicanum*). These are: *P. advena*, *P. anisotomum*, *P. glanduliferum*, *P. mexicanum*, *P. purulhense*, *P. verapazense*, and *P. warszewiczii*.

The low species diversity and the very low endemism in Middle America are perhaps explained by the fact that Central America is rather more remote from existing large land masses to the north and the south, leaving it isolated from the independent evolution that must have been taking place in both of these larger areas (see below for a discussion of the possible origins of the respective species in Central American *Philodendron*). There is strong evidence, at least based on the distribution of modern aroid species, that the northwestern part of Middle America may have been isolated from Costa Rica by the San Juan Depression. Many of the species that occur in Costa Rica or Panama enter into Nicaragua in only a small area in the southeastern part of the country. Although the contemporary flora of Guatemala does not reflect isolation from Mexico to the same degree, it is possible that the more elevated portions of Guatemala, Nicaragua, and Honduras were isolated from major portions of Mexico at the Isthmus of Tehuantepec.

Certainly the Mexican aroid flora appears to be quite isolated, even when compared to the western parts of Middle America (here defined as Guatemala to Nicaragua). Mexico, in addition to having one-third of its species endemic, has relatively few species of *Philodendron* that range throughout Central America. Aside from the aforementioned *P. hederaceum*, only *P. jacquinii*, *P. jodavisianum*, *P. radiatum*, *P. sagittifolium*, and *P. tripartitum* range to northern South America. Two additional species, *P. anisotomum* and *P. mexicanum*, range as far as Panama. Several taxa, *P. advena*, *P. glanduliferum* var. *glanduliferum*, and *P. verapazense*, range only to Guatemala. *Philodendron purulhense* and *P. warszewiczii* range to Honduras, and *P. smithii* ranges to Nicaragua.

Taken together, Honduras and Nicaragua have 21 species of *Philodendron*. Of these, 8 species, *P. advena*, *P. anisotomum*, *P. mexicanum*, *P. radiatum*, *P. sagittifolium*, *P. smithii*, *P. tripartitum*, and *P. warszewiczii*, appear to be of Mexican origin, or in the case of the more widespread and variable species, namely *P. radiatum*, *P. sagittifolium*, and *P. tripartitum*, they may have originated in Panama or Costa Rica and ranged to both Mexico and South America. Certainly, in terms of morphological variation, all of these species are much more variable in Panama and Costa Rica than they are further north. *Philodendron jacquinii* has a circum-Caribbean distribution, indicating that it may be of West Indian origin. It is difficult to determine the origin of *P. hederaceum* given its extensive distribution. Three species, *P. brevispathum*, *P. fragrantissimum*, and *P. tenue*, probably originated in South America considering their widespread distribution there. *Philodendron platypetiolatum*, ranging from Ecuador and barely entering Nicaragua, may be another South American derivative. The remainder, *P. angustilobum*, *P. grandipes*, *P. immixtum*, *P. jodavisianum* (ranging barely to Chiapas and rare there), *P. ligulatum* var. *ligulatum*, *P. pterotum*, *P. rothschuhianum*, and *P. wendlandii*, are probably of Panamanian or perhaps Costa Rican origin.

The Costa Rican and Panamanian species not already discussed above appear not to have strong affinities with South American species, and clearly did not originate in areas of Middle America. Much of the flora of adjacent Nicaragua is closely related to that of Costa Rica. Except for those rather widespread species mentioned above, i.e., *P. brevispathum*, *P. fragrantissimum*, and *P. tenue*, as well as *P. platypetiolatum* (already discussed), there are relatively few species likely to be of South American origin. *Philodendron verrucosum* is almost certainly a South American species, since it is relatively widespread there, occurring on both sides of the Andes. In addition, it seems to have more related species in parts of South America especially in the Andes of western Colombia.

Philodendron dodsonii, which occurs in Ecuador but not Colombia, is just as likely to have originated in South America as in Central America. The same is true of *P. strictum*, which is known from eastern Venezuela and has relatives in the Andes of central Colombia, as well as *P. hebetatum*, which

is rather widespread in western South America as far south as Ecuador. Moreover, the latter apparently does not even reach Costa Rica, making the case for a South American origin even more likely.

Philodendron grandipes, known from western South America as far south as Ecuador, might conceivably be of South American origin despite being very widespread and common as far north as Nicaragua. More probably of South American origin is *P. heleniae*, which is common in Colombia and ranges only to western Panama. Moreover, it seems to have a close relative on the eastern slopes of the Andes.

Three species with scaly parts, *P. malesevichiae*, *P. squamicaule*, and *P. squamipetiolatum*, are moderately rare in Panama, and though all are still poorly known in Colombia, they are more likely to have originated in northwestern Colombia where there are several other relatives with scaly parts.

Some taxa, such as *P. ligulatum* var. *ligulatum*, *P. pseudauriculatum*, and *P. scalarinerve*, either barely enter Colombia or are rare there and are more likely therefore to have originated in Central America. All the remaining species of *P.* subg. *Philodendron* occur in Panama or Costa Rica, with 11 species shared between the two countries.

Taxonomic Treatment

Philodendron ("Philodendrum") Schott, Wiener Z. Kunst. 1829: 780. 1829, nom. et orth. cons. TYPE: *P. grandifolium* (Jacq.) Schott (*Arum grandifolium* Jacq.)

Telipodus Raf., Fl. tellur. 3: 66. 1836[1837]. TYPE: *T. grandifolium* (Jacq.) Raf. (*Arum grandifolium* Jacq.)
Thaumatophyllum Schott, Bonplandia 7: 31. 1859. TYPE: *T. spruceanum* Schott
Elopium H. W. Schott, Oesterr. Bot. Z. 15: 34. 1865. TYPE: *E. surinamense* (Miq.) Schott (*Anthurium surinamense* Miq.)
Baursia T. Post & Kuntze, Lex. gen. phan. 62. 1903. TYPE: *Caladium bauersii* Rchb.

Appressed-climbing or scandent hemiepiphytes, sometimes epiphytes or terrestrial herbs (sometimes stout and arborescent); growth sympodial, anisophyllous, or (more commmonly) diphyllous; trichoschlereids absent, biforines and secretion files present. Leaves with spiral phyllotaxy; petioles rarely geniculate, sheath obsolete or extensive; blades with parallel-pinnate venation, hypostomatic with stomates paracytic, simple to trifoliolate, pinnatifid, bipinnatifid, or (rarely) pedately compound. Inflorescence terminal (appearing axillary), solitary to multiple in leaf axils; spathe enveloping the spadix and constricted or not, usually persistent: spadix monoecious, with sterile male flowers below or both below and (rarely) above the fertile male region; flowers naked, unisexual. Male flowers with 2–6 free stamens, connective enlarged; anther dehiscence by apical slits or pores; pollen inaperturate, boat-shaped, subisopolar, bilaterally symmetrical, shed in monads, medium-sized (mean 40 μm; range 28–54 μm), the exine coarsely verrucate to subfoveolate or (most frequently) psilate; pollen at anthesis binucleate and starch-bearing. Female flowers virtually always lacking staminodes, ovary (2–3)4–6(47)-locular, each locule with axile or (rarely) basal placentation and (1–)4–51 or more orthotropous or hemiantropous, endospermous ovules. Fruit a berry, usually white or orange. Chromosome numbers $2n = 30, 32, 34, 36$. [Description adapted from Grayum (1996).]

Key to *Philodendron* Subgenera

1a. Stem of mature flowering plants with a succession of many leaves terminated by solitary or paired (rarely 3) inflorescences; petioles with long sheaths narrowly encircling the stem at base, winged to at least midway on adult plants; up to 5 leaves produced on the stem between each successive inflorescence ..... subg. *Pteromischum*

1b. Stem of mature flowering plants with a succession of short sympodial segments each bearing a cataphyll and a single leaf with the inflorescence(s) 1 to 10 and appearing to be borne in the leaf axils; petioles of leaves of adult plants with a short, usually inconspicuous petiole sheath borne on the side of the stem, not encircling it at the base (sometimes fully winged on juvenile plants); inflorescences produced with each new leaf (though frequently aborted).

2a. Stems often arborescent, with conspicuous leaf scars and frequently interpetiolar scales persisting around at least the upper margins of the petiolar scars; male flowers conspicuously elongate, up to 10 times longer than wide; staminodial zone between staminate and pistillate zones of the spadix subequal or longer than fertile zone ..... subg. *Meconostigma*

2b. Stems rarely arborescent, often scandent, stout or slender and with interpetiolar scales lacking; male flowers only 2–3 times longer than wide; staminodial zone between staminate and pistillate zones of spadix much shorter than the fertile staminate zone ..... subg. *Philodendron*

Philodendron subg. **Philodendron** Schott. *Philodendron* subg. *Euphilodendron* Engl., Bot. Jahrb. Syst. 26: 509. 1899. *Baursia* subg. *Eubaursia* Kuntze in T. Post & Kuntze, Lex. gen. phan. 62.

Appressed hemiepiphytic climbers or vines with aerial roots, less frequently terrestrial with creeping rhizomatous or deeply rooted stems, rarely short-

stemmed true epiphytes, rarely somewhat arborescent in Central America; sometimes with flagelliform shoots; sap usually tanniniferous and drying dark, rarely with latex and drying white; stems of monophyllous sympodia with elongated hypopodial internodes, densely rooted at nodes; internodes often much longer than broad or about as long as broad, sometimes broader than long at anthesis, sometimes flattened on one side, often coarsely pale-streaked just below the node, usually green and semiglossy, but often turning gray-green to brownish or reddish brown in age; juvenile plants terrestrial or epiphytic and scandent, the petioles conspicuously sheathed and subtended by inconspicuous intravaginal squamulae; cataphylls of mature stems unribbed or variously ribbed, caducous, marcescent and deciduous or persistent and membranaceous to moderately coriaceous, remaining intact or more commonly decomposing to net-like, persistent fibrous reticulum. Leaves usually long-petiolate; petioles usually with ligulate sheath in juvenile plants, on adult plants usually sheathed only at base, variously shaped in cross section, firm or spongy, usually smooth, frequently densely pale-short-lineate or pale-striate throughout, sometimes warty or covered with scale-like processes, rarely geniculate apically; blades simple and entire, ovate, cordate, hastate, sagittate, oblong to elliptic or variously divided, trifid, trifoliolate, or pinnatifid; midrib raised or sunken above, raised below; primary lateral veins pinnate, usually conspicuous, spreading to the margins and running into an antemarginal collective vein; lowermost primary lateral veins (basal veins) often coalesced on cordate blades, the posterior rib (coalesced basal veins) naked along the sinus or not; interprimary veins sometimes present; secondary lateral and higher order veins transversely reticulate between the secondary veins, sometimes all veins slender with no distinct primary lateral veins; minor veins conspicuous or obscure, usually fine and closely parallel; crossveins (minute veins extending transversely between the minor veins) sometimes visible; secretory ducts sometimes appearing like veins, linear, short to long, obscure to very distinct on lower surface. Inflorescences 1–several per axil, usually much shorter than the petioles; peduncles shorter or longer than the spathe; spathe erect, usually coriaceous, entirely persistent, often with large superficial resin canals on inner surface which exude resin, opening widely at anthesis (usually for about one day), then reclosing and persisting in fruit, deciduous only on ripening of fruit, frequently colorful, often bicolorous on outside, typically somewhat constricted between tube and blade, convolute at base; tube cylindric to inflated, uniformly greenish to red or violet-purple within; blade usually opening widely, becoming ± boat-shaped at anthesis, usually white within, sometimes tinged reddish; spadix sessile to stipitate, divided into pistillate and staminate portions, each with unisexual flowers; pistillate zone usually greenish, obliquely fused at its base to the spathe, free above, usually much shorter than the staminate portion and separated from it by a sterile zone of staminodial flowers; intermediate sterile zone cylindric to ellipsoid, much shorter than staminate zone in Central America, usually thicker than staminate zone; staminate zone terete to clavate, white, usually somewhat constricted above the sterile staminate zone; flowers unisexual, naked, closely aggregated in several spirals; staminate flowers 2–6(usually 4–5)-androus; stamens free, adjacent, lacking stomial groove, prismatic to obpyramidal; anthers tetrasporangiate (with microsporangia embedded in the abaxial surface of the anther), columnar in shape, elliptic, ovate to rhombic in cross section, sessile to subsessile; connective thick, apically truncate, usually irregularly 4–5-sided, overtopping thecae; thecae oblong or elliptic, emarginate at the base, dehiscing apically by short, ragged lateral pores; endothecial thickenings lacking; pollen extruded in strands or mixed with resin secretion or exuded in amorphous masses, inaperturate, ellipsoid or oblong or occasionally elongate, medium sized (mean 40 μm, range 28–54 μm), mostly perfectly psilate, sometimes minutely verruculate, scabrate or fossulate to clearly punctate, subfossulate, subfoveolate or subverrucate; sterile staminate flowers naked, usually prismatic, truncate and usually more irregular than fertile flowers and lacking thecae; pistillate flowers with ovary syncarpous, ovoid, subcylindric, cylindric or obovoid, 3–9(14)-locular in Central America (2-locular in *P.* sect. *Philopsammos* in South America); carpels presumably equal to number of locules; placentation axile, sub-basal or basal; ovules 1 to numerous (to ca. 30) per locule, usually hemiorthotropous, rarely hemianatropous, ascending on moderately long or sometimes short funicles; stylar region as broad as or sometimes slightly narrower than ovary; style short, unlobed, with or without boss (see definition under Style Type D), funnel, or annulus; central style dome usually lacking in Central America; stigma sessile, hemispherical to lobulate. Berries subcylindrical to obovoid, exposed by the re-opening of the spathe, white, whitish translucent to red or orange; seeds few to many per berry, oblong to ellipsoid or ovoid-oblong, testa rather thick, striate-costate, rarely sarcotestate; embryo axile, straight, elongate, endosperm copious; chromosomes: $2n = 30, 32, 34, 36, (26, 48)$. Species ca. 700, Central Mexico to Argentina; West Indies (occurring in all countries of Central and South America except Chile and Uruguay).

KEY 1: BLADES DEEPLY LOBED OR DIVIDED 382

KEY 2: BLADES SIMPLE, NON-CORDATE, EITHER OBLONG OR OVATE; SOMETIMES SUBCORDATE TO CORDULATE AT BASE, THE POSTERIOR LOBES UP TO ¼ AS LONG AS ANTERIOR LOBES 383

KEY 3: CORDATE BLADES WITH PERSISTENT CATAPHYLLS 385

KEY 4: VINES WITH CORDATE BLADES AND DECIDUOUS CATAPHYLLS 388

KEY TO *PHILODENDRON* SUBGENUS *PHILODENDRON* OF CENTRAL AMERICA

A. Blades deeply divided, either pinnately lobed, or 3-lobed to trifoliate ..... **KEY 1**

A′. Blades not deeply divided, at most with the margins merely sinuate, the lateral margins of the anterior lobe sometimes deeply concave, but not to such an extent that the blade looks decidedly 3-lobed (blades at first entire, but naturally splitting into irregular segments in *P. findens*).

B. Blades acute, obtuse or truncate at base or sometimes weakly cordulate or subcordate but with the posterior lobes only ¼ as long as the anterior lobe or less ..... **KEY 2**

B′. Blades cordate, sagittate, or hastate at base, the posterior lobes usually more than ¼ as long as the anterior lobes.

C. Cataphylls persistent on stem, either intact or as fibers ..... **KEY 3**

C′. Cataphylls ultimately deciduous, though sometimes persisting ..... **KEY 4**

KEY 1: BLADES DEEPLY LOBED OR DIVIDED

1a. Blades deeply pinnnately lobed, the divisions extending at least ¼ of the way to the midrib.

2a. Leaves bipinnately lobed, the blade divisions near the middle of the blade pinnately lobed, usually divided more than ½-way to the midrib.

3a. Blades lobed only $^{1}/_{10}$–$^{7}/_{10}$ the way to the midrib; Mexico (Sinaloa & Nayarit); 0–370 m ..... *P. dressleri* G. S. Bunting

3b. Blade deeply lobed, the divisions extending more than $^{7}/_{10}$ of the way to the midrib.

4a. Blades deciduous during the dry season; leaf segments thin, drying papyraceous, pale yellow-green to yellow-brown, with the minor veins distinctly visible and darker than surface; lateral segments with usually 3 or more lobes per side, extending to below the middle of the pinnae; Mexico (Jalisco & Chiapas) to El Salvador, Guatemala, Honduras, and Nicaragua, 300–1500 m ..... *P. warszewiczii* K. Koch & Bouché

4b. Blades evergreen; leaf blade segments subcoriaceous, drying moderately thick, dark brown or sometimes reddish brown, the minor veins not distinctly visible on drying, not markedly darker than surface; lateral segments with usually 1–2 lobes per side, usually restricted to near the apex of the pinnae; Mexico to Colombia, 0–700, rarely to 1860 m ..... *P. radiatum* var. *radiatum*

2b. Leaves merely pinnately lobed, the blade divisions near the middle of the blade not pinnately lobed, or, if so, divided less than ½-way to the midrib ..... *P. radiatum* var. *pseudoradiatum* Croat

1b. Blades deeply 3-lobed or trifoliate.

5a. Blade with the medial lobe less than 1.7 times longer than the lateral lobes; lateral lobes directed ± toward the apex.

6a. Lateral lobes of the blade broadly confluent with the medial lobe by at least 2 cm from the base of the blade (as measured from the depths of the incised area and the apex of the petiole); inflorescences usually 3–9 per axil.

7a. Medial lobe of the blade with 5–12 pairs of primary lateral veins; spathe tube uniformly greenish to whitish within; Honduras to Panama, usually below 1000 m ..... *P. rothschuhianum* (Engl.) Croat & Grayum

7b. Medial lobe of the blade with 18–19 pairs of primary lateral veins; spathe tube red-violet or purplish within; Costa Rica (Puntarenas, San José), 1000–1250 m ..... *P. cotobrusense* Croat & Grayum

6b. Lateral lobes of the blade not confluent with or only weakly confluent with the medial lobe to no more than 1 cm from the base of the blade; inflorescences usually 1, rarely to 3 per axil.

8a. Medial lobe of blades with more than 18 pairs of primary lateral veins, elliptic; central Panama, 350–450 m ..... *P. madronense* Croat

8b. Medial lobe of blade with fewer than 12 pairs of primary lateral veins, usually oblanceolate to oblong-lanceolate; widespread species, Mexico to Ecuador.

9a. Medial lobe mostly 3–3.5 times longer than broad (rarely as little as 1.7 times longer than broad); primary lateral veins of medial lobe 4–12 per side, prominently sunken; lateral lobes directed ± toward the apex; minor veins arising from both the midrib and the primary lateral veins; ripe fruits whitish; Mexico to Ecuador, 0–1300(1500) m ..... *P. tripartitum* (Jacq.) Schott

9b. Medial lobe mostly 1.5–2 times longer than broad; primary lateral veins of medial lobe mostly 2–4, rarely 5 per side, weakly sunken; lateral lobes directed ± outward; minor veins arising only from the midrib; ripe fruits orange; Mexico to Costa Rica, 30–1800 m ..... *P. anisotomum* Schott

5b. Blades with the medial lobe more than 1.7 times longer than the lateral lobes; lateral lobes directed laterally (spreading) outward or even downward toward the base of the petiole (reflexed).
10a. Blades sagittate, the lateral lobes directed downward somewhat toward the base of blade (in direction of petiole); Mexico to Panama and South America, 0–1900 m ..... *P. mexicanum* Engl.
10b. Blades hastate, the lateral lobes directed outward at ca. 90° angle.
11a. Lateral lobes confluent with the medial lobe by usually for more than 4 cm (rarely to 3.3 cm); basal veins 8–10 per side; Honduras to Panama, 0–680 m ..... *P. angustilobum* Croat & Grayum
11b. Lateral lobes confluent with the medial lobe by usually less than 3 cm (rarely to 8 cm); basal veins 4–7 per side; Mexico to Costa Rica, 30–1800 m ..... *P. anisotomum* Schott

KEY 2: BLADES ENTIRE OR SHALLOWLY DIVIDED, NON-CORDATE, EITHER OBLONG OR OVATE; SOMETIMES SUBCORDATE OR CORDULATE AT BASE, THE POSTERIOR LOBES UP TO ¼ AS LONG AS ANTERIOR LOBES

1a. Plants vines or at least with internodes much longer than broad.

VINES OR SCANDENT: INTERNODES MUCH LONGER THAN BROAD; BLADES OVATE

2a. Blades ± ovate, less than 2 times longer than wide.
3a. Blades with primary lateral veins either 2 or fewer or with the primary lateral veins inconspicuous, scarcely more distinct than the minor veins.
4a. Blades more than 11 cm wide; peduncles more than 10 cm long; Costa Rica, 50–450 m..... *P. microstictum* Standl. & L. O. Williams
4b. Blades less than 11 cm wide; peduncles less than 10 cm long.
5a. Internodes less than 10 cm long; blades less than 1.4 times longer than wide, drying greenish, lacking primary lateral veins; Panama, Cerro Brewster, 850 m ..... *P. brewsterense* Croat
5b. Internodes more than 10 cm long; blades ca. 2 times longer than wide, drying brown, with up to 2 obscure primary lateral veins; Costa Rica, Río Chirripó del Pacífico, San José Prov., 1000 m ..... *P. chirripoense* Croat & Grayum
3b. Blades with the primary lateral veins more than 2 and much more prominent than the minor veins.
6a. Blades ovate to broadly ovate, mostly less than 1.7 times longer than wide.
7a. Stems, petioles, and inflorescences densely scaly (petiolar scales slender and spreading); major veins on lower surface densely puberulent; Panama to Ecuador, 0–1300 m ..... *P. squamipetiolatum* Croat
7b. Stems, petioles, and inflorescences glabrous; major veins on lower surface glabrous; Panama (Coclé, Veraguas), 770–1200 m ..... *P. ligulatum* var. *ovatum* Croat
6b. Blades narrowly ovate to oblong-elliptic, usually more than 2 times longer than wide.
8a. Blades less than 12 cm wide; posterior lobes about as long as broad; Panama to Colombia, 0–140 m ..... *P. immixtum* Croat
8b. Blades usually more than 12 cm wide; posterior lobes much broader than long; Costa Rica to Panama, (210)670–1800 m ..... *P. lentii* Croat & Grayum
2b. Blades ± oblong to oblong-elliptic (rarely narrowly ovate) or oblanceolate, usually more than 2.5 times longer than wide.

VINES WITH ± OBLONG BLADES

9a. Blades lacking distinct primary veins at base of blade; primary lateral veins obscure or lacking.
10a. Blades drying gray-green; primary lateral veins not at all apparent; Panama (San Blas), near sea level ..... *P. ubigantupense* Croat
10b. Blades drying reddish brown or blackened; primary lateral veins 3–6, obscure but still visible.
11a. Blades drying blackened, usually more than 25 cm long; spathe more than 12 cm long; Panama (Bocas del Toro and Chiriquí), 780–1400 m ..... *P. correae* Croat
11b. Blades drying reddish brown, usually less than 25 cm long; spathe less than 12 cm long; Costa Rica (100–900 m) to Panama, 900–1420 m ..... *P. bakeri* Croat & Grayum
9b. Blades with one or more distinct primary veins at base of blade; primary lateral veins distinct.
12a. Petioles encircled distally with a dark purplish (or dark green) ring separating the petiole and the blade.
13a. Blades with posterior lobes usually narrowly rounded and somewhat spreading or broader than long, rarely about as long as broad; inflorescences 1–3 per axil; Panama, 100–970 m ..... *P. annulatum* Croat
13b. Blades with posterior lobes about as broad as long and held closely near the petiole; inflorescence usually solitary (sometimes 2 in *P. immixtum*).
14a. Blades typically drying greenish to greenish brown, rarely more than 30 cm long; Panama to Colombia, 0–140 m ..... *P. immixtum* Croat
14b. Blades typically drying blackened, rarely less than 30 cm long; Nicaragua to Colombia, 0–1200 m ..... *P. ligulatum* Schott var. *ligulatum*
12b. Petioles lacking a dark purple distal ring.

15a. Blades less than 10 cm wide; stem minutely pale granular-puberulent at high magnification; pistil with a funnel-shaped stigma (type E); ovules 1 per locule; Panama (Darién), 75 m ..... *P. granulare* Croat

15b. Blades usually more than 15 cm wide (rarely to as little as 10 cm wide in *P. heleniae*); stems smooth to irregularly ridged or folded at high magnification (sometimes minutely warty but not pale granular-puberulent); pistil with a flat style apex (type B); ovules 3 or more per locule.

16a. Blades drying coriaceous, lacking secretory ducts; spathes greenish white to white outside, more than 10 cm long; Costa Rica to Panama, (210)670–1800 m ..... *P. lentii* Croat & Grayum

16b. Blades drying subcoriaceous, with conspicuous secretory ducts; spathes red outside, mostly less than 10 cm long; Panama and Ecuador, mostly 100–1040 m ..... *P. heleniae* Croat

1b. Plants appressed-climbing or sometimes terrestrial, with the internodes typically broader than long or only slightly longer than broad.

NON-VINING PLANTS; BLADES OBLONG

17a. Cataphylls deciduous.

18a. Blades usually prominently lobed at base, the lobes typically longer than broad or at least usually spreading away from the petiole.

19a. Blades thin-drying; sinus arcuate with blade tissue somewhat decurrent on petiole; petiole drying 2–4 mm diam.; Panama, E of Canal Area, 450–850 m ..... *P. morii* Croat

19b. Blades thick-drying; sinus oblong to parabolic or arcuate but with blade tissue not at all decurrent onto petiole; Panama, 100–970 m ..... *P. annulatum* Croat

18b. Blades not lobed at base or merely cordulate with posterior lobes round, as broad as long, held closely against the petioles.

20a. Largest leaf blades more than 50 cm long.

21a. Blades usually more than 30 cm wide; petioles usually about 85% the length of the blades or even longer than the blades; Costa Rica and Panama, 0–200 m ..... *P. davidsonii* Croat

21b. Blades less than 30 cm wide; petioles typically much shorter than the blade.

22a. Blades drying reddish brown, 4.4–4.9 times longer than wide; petioles lacking a purple distal ring; Panama, 325–650 m ..... *P. dolichophyllum* Croat

22b. Blades drying dark gray-green to blackened, usually less than 4.3 times longer than wide; petiole with a purple or green distal ring.

23a. Petioles subterete adaxially, not at all winged marginally; Panama and Colombia, 20–1400 m ..... *P. pseudauriculatum* Croat

23b. Petioles sharply D-shaped with slender wings on the adaxial margins; Panama, Darién, 50–200 m ..... *P. ligulatum* var. *heraclioanum* Croat

20b. Largest leaf blades usually less than 50 cm long.

24a. Blades usually drying green to yellowish green, thin.

25a. Blades oblong-lanceolate, less than 7 cm wide, obtuse to almost rounded at base and then decurrent along petiole; Panama (Coclé), 700–800 m .... *P. folsomii* Croat

25b. Blades ovate-triangular, 11–16 cm wide, subcordate at base; eastern Panama, 450–850 m ..... *P. morii* Croat

24b. Blades drying yellow-brown or brownish, gray-brown to reddish brown, moderately coriaceous.

26a. Inflorescences 2–10 per axil; peduncle less than 6 cm long; spathe tube reddish maroon outside and within; leaf blades with conspicuous secretory ducts visible on the lower dried surface; Panama to Colombia and Ecuador, 20–1040(1450) m ..... *P. heleniae* Croat

26b. Inflorescence solitary; peduncle ca. 9 cm long; spathe tube green outside, white within; leaf blades lacking any sign of secretory ducts; Panama (Colón), ca. 200 m ..... *P. utleyanum* Croat

17b. Cataphylls persistent.

27a. Plants usually terrestrial and rosulate; petioles deeper than wide; blades usually elliptic to oblong-elliptic, acute to narrowly rounded at base; Panama to Colombia, 100–1000 m ..... *P. roseospathum* Croat

27b. Plants epiphytic to hemiepiphytic, not rosulate; petioles as deep as wide; blades linear to oblanceolate or oblong-elliptic, sometimes weakly cordate to cordulate at base.

28a. Blades linear to oblanceolate, attenuate at base; primary lateral veins arising at 25–45° angle from midrib; cross-veins not visible on drying; sap chalky white; Costa Rica to Panama, 0–900 m ..... *P. cretosum* Croat & Grayum

28b. Blades oblong-elliptic to narrowly ovate, obtuse to subcordate at base; primary lateral veins arising at 60–75° angle; cross-veins very conspicuous on drying; sap not colored, or if so not white; Costa Rica to Colombia, 0–1325 m ..... *P. scalarinerve* Croat & Grayum

29a. Blades usually broadest above the middle, acute, obtuse, narrowly rounded to merely minutely cordulate at base.

30a. Petioles sharply flattened adaxially (with acute lateral margins); blades acute to narrowly rounded (never cordulate) at base, mostly more than 2.5 times longer

than petioles; internodes broader than long; Costa Rica, Nicaragua, and Panama, Atlantic slope; 10–1250 m ..... *P. wendlandii* Schott

30b. Petioles subterete; blades narrowly cordulate at base, less than 1.8 times longer than petioles; internodes often longer than broad; southwestern Costa Rica, Pacific lowlands, 0–1200 m ..... *P. auriculatum* Standl. & L. O. Williams

29b. Blades broadest below the middle, cordate to subcordate at base (acute to truncate in *P. davidsonii* subsp. *bocatoranum*).

31a. Blades ovate to broadly ovate, less than 60 cm long, drying dark brown; primary lateral veins 5–9 per side; petioles terete; Panama (Darién), ca. 1500 m ..... *P. niqueanum* Croat

31b. Blades ovate-oblong, usually more than 60 cm long, drying light brown; primary lateral veins 18–21 per side; petioles thicker than broad (i.e., with the thickest dimension perpendicular to the plane of the blade) and broadly sulcate adaxially; Costa Rica to Panama, 0–200 m ..... *P. davidsonii* Croat

KEY 3: CORDATE BLADES WITH PERSISTENT CATAPHYLLS

1a. Blades with posterior rib (union of basal veins) naked along the edge of the sinus.

2a. Petioles with conspicuous, elongate, hair-like scales.

3a. Petiolar scales scattered and mostly in the distal ½ of petiole; plants terrestrial; Panama and Colombia, 830–860 m in Panama, 50–150 m in Colombia ..... *P. malesevichiae* Croat

3b. Petiole scales dense, covering the entire petiole; plants usually hemiepiphytic.

4a. Blades ovate-triangular, typically more than 1.3 times longer than broad, semiglossy above, paler and solid light green to silvery-green beneath, Costa Rica to Ecuador, <100–1250 m ..... *P. squamicaule* Croat & Grayum

4b. Blades ovate, typically less than 1.3 times longer than broad, matte and subvelvety above, paler and tinged with purplish violet between the major veins below; Costa Rica to Peru, (200)500–1500 m ..... *P. verrucosum* L. Mathieu ex Schott

2b. Petioles glabrous or least lacking scales.

5a. Petioles conspicuously and sharply flattened adaxially, with lateral margins sharply edged or with a slender wing.

6a. Petioles merely sharply edged, lacking an actual wing at the margin.

7a. Blades whitish and matte below; cataphylls persisting in semi-intact fragments of thin epidermis; spathe tube green outside, at most tinged pink within; Costa Rica to Panama (Chiriquí), (775)1000–2100 m ..... *P. thalassicum* Croat & Grayum

7b. Blades green and semiglossy below; cataphylls persisting in a dense reddish brown, semi-intact mass; spathe tube green or bright red outside, dark red to maroon within, blade white; Belize to South America, 0–900 m.

8a. Blades ovate-triangular, 1.8–2.7 times longer than wide; cross-veins conspicuous between minor veins on dried blades; spathe tube green on outside; W Panama (Bocas del Toro to Coclé), 590–1300 m ..... *P. copense* Croat

8b. Blades mostly ovate, 1.1–1.7 times longer than wide; cross-veins between minor veins not at all apparent; spathe tube bright red outside; Belize to South America, 0–1000 m ..... *P. fragrantissimum* (Hook.) G. Don

6b. Petioles with a narrow marginal wing.

9a. Leaf blades promptly splitting into slender segments laterally, drying blackened; petiole wing undulate distally; Costa Rica to Panama, Atlantic slope, 0–1400 m ..... *P. findens* Croat & Grayum

9b. Leaf blades remaining intact, drying yellow-green; petiole wing usually undulate throughout its entire length; Nicaragua to central Panama, mostly less than 700 m ..... *P. pterotum* K. Koch & Augustin

5b. Petioles terete to obtusely flattened or U-shaped but not sharply flattened adaxially, if sulcate adaxially the margins merely obtuse.

10a. Blades whitish and matte on lower surface even on fresh leaves; petioles usually drying light yellowish brown (except sometimes not in *P. strictum*).

11a. Blades narrowly ovate, usually more than 1.8 times longer than wide; plants commonly hemiepiphytes; Panama to Ecuador, usually <1400 m ..... *P. hebetatum* Croat

11b. Blades ovate to broadly ovate, averaging 1.3 times longer than wide; typically terrestrial; Costa Rica to western Panama, Colombia, and Venezuela, mostly at 850–1665 m in Central America ..... *P. strictum* G. S. Bunting

10b. Blades green to yellow-green beneath, usually semiglossy to glossy; petioles drying various colors, not light yellowish brown (except *P. copense*, *P. schottianum*, and *P. thalassicum*).

NARROWLY OVATE BLADES

12a. Blades usually 1.8 times or more longer than wide.

13a. Spathe tube greenish to yellow-green or whitish inside.

14a. Leaf blades with lower surface matte, frequently bluish green; style apex prolonged into a short but distinct neck (style type D); central Costa Rica to western Panama, (775)1000–2100 m ..... *P. thalassicum* Croat & Grayum

14b. Leaf blades with lower surface glossy to semiglossy, not at all bluish green; style apex flat, not prolonged into a distinct neck (style type B; rarely type C); Panama, except *P. jodavisianum* (Mexico to Venezuela).

15a. Blades drying yellow-green; basal veins fewer than 5; sap milky white, drying chalky; inflorescence solitary; cataphylls to 40 cm long; Panama (Darién), 800–1480 m ..... *P. albisuccus* Croat

15b. Blades drying dark gray-brown to olive-green, typically somewhat blackened; basal veins usually more than 5; sap usually clear, drying dark brown to reddish; inflorescences 2–6 per axil; cataphylls less than 20 cm long.

16a. Petioles terete to obtusely flattened adaxially, lacking prominently raised lateral margins; peduncles frequently longer than the spathe; central and eastern Panama, 0–800 m ..... *P. panamense* K. Krause

16b. Petioles usually D-shaped or U-shaped, usually flattened adaxially with prominently raised margins, often thicker than broad, rarely C-shaped to subterete; peduncles usually much shorter than the spathe; S Mexico to Panama and Venezuela (Mérida), 0–1500 m ..... *P. jodavisianum* G. S. Bunting

13b. Spathe tube red to maroon or violet-purple on inside.

17a. Blades drying greenish to yellow-green (sometimes yellow-brownish in *P. alticola*), lacking conspicuous cross-veins.

18a. Pistils with 1 ovule per locule; leaf blades with secretory ducts moderately obscure, the abaxial surface densely and minutely granular on drying; staminate portion of the spadix constricted above the sterile portion, the fertile portion clavate, the sterile staminate portion only slightly thicker than the pistillate portion; dried style base doughnut-shaped with stylar canals at the bottom of a deep concavity; Panama (Chiriquí to Coclé, (750) 950–2200 m) and Costa Rica ..... *P. straminicaule* Croat

18b. Pistils with 12–18 ovules per locule; leaf blades with secretory ducts conspicuous, abaxial surface smooth on drying; staminate portion of the spadix scarcely constricted above the sterile portion, the fertile portion stubby and evenly tapered to the apex, the sterile staminate portion much thicker than the pistillate (approximately ⅓ thicker); dried style base raised but flattened at apex with a narrow pale ring around its outer margin, the stylar canals exserted like minute funnels and extending above the surface; eastern Costa Rica and western Panama, 800–2500 m ..... *P. alticola* Croat & Grayum

17b. Blades drying reddish brown with conspicuous cross-veins.

19a. Petioles drying with a conspicuous light reddish brown or yellow-brown epidermis, this smooth and often flaking; cataphylls less than 25 cm long; primary lateral veins 11–16 per side; basal veins frequently more than 8 per side; Panama (Bocas del Toro and Coclé Provinces), 590–930 m ..... *P. copense* Croat

19b. Petioles drying dark brown, the epidermis not peeling; cataphylls more than 55 cm long; primary lateral veins fewer than 8 per side; basal veins up to 8 per side; Panama (Chiriquí, Bocas del Toro, Coclé, and Veraguas Provinces), 500–1630 m ..... *P. chiriquense* Croat

OVATE TO BROADLY OVATE BLADES

12b. Blades usually about 1.5 times longer than wide or less (sometimes wider than long).

20a. Leaf blades with lower surface matte (but never velvety), frequently bluish green, the dried waxy surface forming an areolate pattern; central Costa Rica to western Panama, (775)1000–2100 m ..... *P. thalassicum* Croat & Grayum

20b. Leaf blades with lower surface semiglossy (or, if matte, then velvety), never bluish green.

21a. Leaf blades matte and velvety above; central Panama in the region of the isthmus, 300–375 m ..... *P. gigas* Croat

21b. Leaf blades semiglossy to glossy above.

22a. Peduncles usually less than 10 cm long (rarely longer in fruiting peduncles of *P. llanoense* and *P. dodsonii*).

23a. Spathe tube solid bright red on outside; central Panama (Veraguas and Coclé), 800–1200 m ..... *P. antonioanum* Croat

23b. Spathe tube green outside (sometimes tinged weakly red on *P. schottianum*).

24a. Spathe weakly or not at all constricted above the tube.

25a. Cataphylls persisting usually with large fragments of glossy, yellowish epidermis; petioles drying yellowish to yellowish brown and glossy as if with a layer of shellac; Costa Rica to Panama, 600–2200 m ..... *P. schottianum* H. Wendl. ex Schott

25b. Cataphylls persisting semi-intact and brown, not glossy or yellowish; petioles usually drying brown to blackened, usually not yellowish and glossy; Guatemala, 1360–1870 m ..... *P. purulhense* Croat

24b. Spathe moderately to prominently constricted above the tube.

26a. Leaf blades drying yellow-brown below, coriaceous; ovules mostly (6)12–(20) per locule; Isthmus of Panama, mostly below 500 m ..... *P. llanense* Croat

26b. Leaf blades drying reddish brown, moderately thin; ovules 1–6 per locule (except *P. dodsonii* with ca. 20 ovules per locule); Costa Rica or Mexico.

27a. Stems usually growing over rocks in dry habitats, rarely on trees; cataphylls eventually deciduous, intact on the older stem; ovules 4–6 per locule; western Mexico (Jalisco & Guerrero), 350–1250 m ..... *P. basii* Matuda

27b. Stems appressed-climbing on trees in humid habitats; cataphylls decomposing and breaking up before falling off; ovules either solitary or ca. 20 per locule; Costa Rica and/or Ecuador.

28a. Spathe tube green; ovules 1 per locule; posterior rib barely or not at all naked along the sinus (up to at most 2.5 cm); southwestern Costa Rica, 1000 m ..... *P. dominicalense* Croat & Grayum

28b. Spathe tube dark reddish to red-purple; ovules ca. 20 per locule; posterior rib naked to ca. 6 cm along the sinus; Costa Rica, principally on the Atlantic slope at 300–850 m and Colombia and Ecuador at 200–1300 m ..... *P. dodsonii* Croat & Grayum

22b. Peduncles usually more than 10 cm long (rarely less than 10 cm long) when not at anthesis.

29a. Stems clothed with a dense series of overlapping cataphylls, each persisting as a reticulum of coarse fibers often overlain with a thin, fragmented epidermis.

30a. Blades 1.2–1.5 times longer than wide, drying reddish brown above; Panama (Darién), 1000–1560 m ..... *P. pirrense* Croat

30b. Blades 0.8–1.4 times longer than wide, drying grayish green above.

31a. Dried blades with lower surface semiglossy, sparsely granular, with moderately conspicuous cross-veins, not speckled, the upper surface lacking raphide cells; ovules 6 per locule; Panama, Panama Province (Cerro Jefe), 550–800 m ..... *P. jefense* Croat

31b. Dried blades with lower surface matte, smooth and minutely brownish to whitish speckled, lacking obvious cross-veins, the upper surface usually with short whitish raphide cells visible; ovules 14–20 per locule; Panama, Canal Area to Darién Province (Cerro Sapo), 140–800 m ..... *P. lazorii* Croat

29b. Stems with only a few cataphylls, these usually semi-intact or with a few, thin, disorganized fibers.

32a. Blades drying reddish brown to dark yellow-brown; peduncles usually less than half as long as the spathe, straight below the spathe; spathe tube reddish purple to red outside; Costa Rica, Colombia, and Ecuador, 200–1300 m ..... *P. dodsonii* Croat & Grayum

32b. Blades drying dark gray-brown to olive-green, typically somewhat blackened above; peduncles usually as long as or longer than the spathe, frequently bent just below the spathe; spathe tube greenish on outside; Panama, 0–800 m ..... *P. panamense* K. Krause

1b. Blades with posterior rib (union of basal veins) not naked along the sinus, flanked with laminar tissue.

33a. Petioles conspicuously scaly distally; terrestrial (except *P. verrucosum*).

34a. Blades less than 25 cm long; petiolar scales close and overlapping, broad, usually less than 3 times longer than wide; endemic to El Copé region of Panama, ca. 800 m ..... *P. hammelii* Croat

34b. Blades usually more than 30 cm long; petiolar scales more widely scattered, many times longer than wide.

35a. Plants terrestrial; stems usually creeping laterally across the ground; spathes glabrous; Mexico and Guatemala, 580–1900 m ..... *P. glanduliferum* Matuda subsp. *glanduliferum*

35b. Plants appressed hemiepiphytic climbers; stems usually climbing trees; spathes conspicuously covered with slender scales, Costa Rica to Peru, 200–1500 m (mostly >500 m) ..... *P. verrucosum* L. Mathieu ex Schott

33b. Petioles glabrous and smooth distally, at least not conspicuously scaly; usually hemiepiphytic.

36a. Plants consistently terrestrial; petioles D-shaped with raised margins and a medial rib; spathe tube greenish to whitish within (or usually reddish on Pacific slope of Costa Rica); Nicaragua (Zelaya) to Panama, Colombia, and Ecuador; mostly 0–750 m ..... *P. grandipes* K. Krause

36b. Plants usually hemiepiphytic (*P. tysonii* frequently terrestrial in some habitats); petioles terete to subterete; spathe tube maroon to red or violet-purple within.

37a. Spathe not at all constricted above the tube, the spathe wall usually to ca. 1 cm thick midway; leaf blades very coriaceous, minor veins etched in the upper surface of fresh leaves; central Costa Rica to western Panama, 1100–2600 m ..... *P. crassispathum* Croat & Grayum

37b. Spathe visibly constricted above the tube (except only weakly constricted for *P. antonioanum*), the wall usually less than 3 mm thick except at very base; leaf blades not markedly coriaceous, minor veins never etched into surface of fresh leaves.

38a. Primary lateral veins frequently 10 or more per side; spathe tube white to pale green within (sometimes tinged red at very base); Nicaragua to S Ecuador and to Venezuela; 20–1400 m ..... *P. tenue* K. Koch & Augustin

38b. Primary lateral veins usually fewer than 10 per side (to 10 in *P. tysonii*); spathe tube red to red-violet, maroon, or violet-purple throughout within.

39a. Blades markedly sinuate along the margins; Mexico (Veracruz), less than 500 m ..... *P. subincisum* Schott

39b. Blades with the margins entire, not at all sinuate.

40a. Fresh cataphylls usually red; petioles and midribs lacking conspicuous purplish spots; basal veins 5–10 per side.

41a. Blades with primary lateral veins typically 6–10 per side, upper surface drying somewhat blackened and smooth; cataphylls unribbed to weakly 1-ribbed; spathe tube green or merely tinged reddish outside; ovaries with fewer than 7 sub-basal ovules contained in an ovule sac; western and central Panama, 600–1500 m ..... *P. tysonii* Croat

41b. Blades with primary lateral veins usually 5–6 per side, upper surface drying dark brown to gray-brown with prominulous cross-veining; cataphylls sharply 2-ribbed; spathe tube dark maroon outside; ovaries with about 30 axile ovules not contained in an envelope; endemic to Veraguas and Coclé Provinces at 850–1150 m ... *P. antonioanum* Croat

40b. Fresh cataphylls green (purplish-spotted in *P. edenudatum* and *P. grayumii*); petioles and midrib frequently purplish-spotted; basal veins usually 3–5 per side.

42a. Blades mostly more than 1.8 times longer than wide; petioles 0.85–0.90 times as long as the blade; dried blades without secretory ducts visible on lower surface; Panama, 110–1150 m ... *P. edenudatum* Croat

42b. Blades mostly less than 1.8 times longer than wide; petioles 1–1.4 times longer than the blade; dried blades with secretory ducts clearly visible on the lower surface; Costa Rica to central Panama, 0–1630 m ..... *P. grayumii* Croat

Key 4: Vines with Cordate Blades and Deciduous Cataphylls

[Note: None of the species in this group have the posterior rib of the leaf blades naked along the sinus except *P. brunneicaule, P. hederaceum, P. mexicanum,* and sometimes (weakly so) *P. coloradense, P. cotonense, P. sulcicaule, P. wilburii,* and *P. zhuanum.*]

1a. Internodes elongate, usually much longer than broad; plants usually vines or at least prominently scandent.

2a. Blades with the posterior rib (coalesced basal veins) not naked (i.e., not running on the margin of the sinus).

3a. Stems coarsely asperous, covered with branched scales or setose-pubescent.

4a. Blades ovate-triangular, subcoriaceous; posterior lobes slender, usually flaring; stems reddish brown, covered with trichome-like, frequently branched scales; berries pale yellow; styles very short; occurring usually in wet habitats; Nicaragua to Panama and South America, 60–280(1300) m ..... *P. brevispathum* Schott

4b. Blades ovate-cordate, thin; posterior lobes directed toward one another at maturity; stems greenish, covered with elongate setae; berries pale orange to red or reddish orange; usually occurring in dry habitats; Mexico to Panama, the West Indies, and South America, 0–1500(2500) m ..... *P. jacquinii* Schott

3b. Stems smooth, not covered with branched scales.

5a. Petioles prominently flattened dorsiventrally with the lateral margins sometimes acute; Nicaragua to Ecuador, 10–1500 m ..... *P. platypetiolatum* Madison

5b. Petioles terete to subterete, not prominently flattened dorsiventrally.

6a. Peduncles usually much shorter than the spathe, usually less than 7 cm long at anthesis, drying 6–10 mm diam.; ovules many (usually 10–20) per locule.

7a. Leaf blades narrowly ovate-elliptic or triangular-sagittate or triangular-hastate, usually 1.8 times or more longer than wide; posterior rib more than 3 cm long.

8a. Leaf blades narrowly ovate-elliptic; posterior lobes about as broad as long, directed toward the base; sinus ± V-shaped; ovules ca. 20 per locule; Mexico (Chiapas), 0–1000 m ..... *P. breedlovei* Croat

8b. Leaf blades triangular-sagittate to triangular-hastate; posterior lobes typically much longer than broad, directed somewhat outward; sinus usually not V-shaped but parabolic to spathulate; ovules usually 1–2 per locule; Mexico to Colombia, 0–1900 m ..... *P. mexicanum* Engl.

7b. Leaf blades ovate, usually only slightly longer than wide (rarely to 1.9 times longer than wide in *P. hederaceum*); posterior rib virtually lacking or to at most 1 cm long.

9a. Stems drying dark reddish brown, prominently ribbed, usually densely warty; Costa Rica to Ecuador and Suriname; (250)300–900 m ..... *P. hederaceum* var. *kirkbridei* Croat

9b. Stems drying either green and only weakly striate, or light yellowish brown and deeply fissured on drying.

10a. Stems drying yellowish brown, prominently ridged, smooth and glossy; spathe tube violet-purple outside; Costa Rica to Ecuador, 0–1600 m ..... *P. purpureoviride* Engl.

10b. Stems drying greenish, weakly striate, matte; spathe tube green outside; Mexico to West Indies, widespread in South America ..... *P. hederaceum* (Jacq.) Schott

6b. Peduncles frequently as long as or longer than the spathe, sometimes more than 7 cm long, usually drying 3–4 mm diam.; ovules 1 or 2 per locule.

11a. Leaf blades lacking any obvious primary lateral veins; stems prominently sulcate-ribbed even when fresh; ovules 1 per locule; SE Costa Rica to central Panama; 100–700 m ..... *P. sulcicaule* Croat

11b. Leaf blades with obvious primary lateral veins; stems smooth (or at least not regularly and prominently sulcate-ribbed longitudinally when fresh); ovules 2 per locule; Panama (Darién); 850–1560 m ..... *P. clewellii* Croat

CORDATE VINES WITH DECIDUOUS CATAPHYLLS AND BLADES WITH NAKED POSTERIOR RIBS

2b. Blades with the posterior rib naked and running on the margin of the sinus for usually 1.5 cm or more (sometimes to as little as 1 cm in *P. smithii*).

12a. Stems setose-pubescent; blades membranaceous on drying; spathe tube inflated, with considerable space between the inner surface of the spathe and the spadix; pistils elongated at apex into a style to ca. 5 mm long; Mexico to Panama, Cuba, and northern South America; 0–1500(2500) m ..... *P. jacquinii* Schott

12b. Stems glabrous; blades coriaceous to subcoriaceous on drying; spathe not inflated-bulbous at base, fitting tightly over spadix; pistils not at all elongated into a distinct stylar region.

13a. Stems prominently and regularly sulcate-ribbed when fresh.

14a. Blades less than 24 cm long, lacking obvious primary lateral veins; petioles to 21 cm long; NE Costa Rica to Isthmus of Panama; 100–700 m ..... *P. sulcicaule* Croat

14b. Blades more than 26 cm long, with 3–4 obvious pairs of primary lateral veins; petioles more than 29 cm long; S Mexico to Guatemala; 700–1525 m ..... *P. verapazense* Croat

13b. Stems smooth or irregularly fissured but not regularly sulcate-ribbed when fresh.

15a. Blades mostly broadly ovate, usually more than 25 cm wide; posterior lobes usually broadly rounded, about as wide as long; stems drying light reddish brown with flaking epidermis; Costa Rica to Ecuador, 100–1300 m ..... *P. brunneicaule* Croat & Grayum

15b. Blades mostly ovate-triangular or triangular-sagittate to triangular-hastate, mostly less than 25 cm wide (sometimes broader in *P. smithii*); Mexico to Panama; 0–2000 m.

16a. Blades sagittate to hastate at base; posterior lobes 2–3 times longer than broad; posterior rib directed straight toward the apex of the posterior lobe and 1.5–3.5 cm distant from the posterior margin of the blade; Mexico to Panama, 0–1900 m ..... *P. mexicanum* Engl.

16b. Blades cordate or sagittate (rarely hastate in some forms of *P. wilburii*); posterior lobes usually less than 2 times longer than wide (except sometimes more than 2 times longer in *P. wilburii*, and then blades drying reddish brown, not greenish as in *P. mexicanum*); posterior rib mostly curved along and near the margin of the sinus, rarely more than 1 cm from the posterior margin of the blade.

17a. Cataphylls 2-ribbed; blades usually more than 35 cm long; petiole often with a purple distal ring; peduncle usually longer than the spathe; Mexico to Nicaragua, 40–1630 m ..... *P. smithii* Engl.

17b. Cataphylls 1-ribbed (rarely 2-ribbed); blades usually less than 36 cm long; petioles lacking a purple distal ring; peduncle usually shorter than the spathe (except often longer in *P. wilburii* var. *longipedunculatum*); central Costa Rica to central Panama, 0–2000 m ..... *P. wilburii* Croat & Grayum

CORDATE NON-VINES WITH DECIDUOUS CATAPHYLLS AND NON-NAKED POSTERIOR RIBS

1b. Internodes of mature stems broader than long or sometimes somewhat longer than broad but not elongate with scandent stems (possibly somewhat scandent in *P. breedlovei* and *P. sousae*); plants mostly appressed-climbing hemiepiphytes.

18a. Petioles either densely covered with scales or D-shaped with undulate-winged margins.

19a. Petioles terete, less than 1 cm diam., densely covered with conspicuous, spreading scales; blades almost as broad as long, the major veins on the lower surface densely puberulent; Panama to Ecuador; 0–1300 m ..... *P. squamipetiolatum* Croat

19b. Petioles sharply D-shaped or sharply flattened with undulate-winged margins, more than 1.5 cm diam., glabrous; blades much longer than broad; veins of lower surface glabrous; Panama (Chiriquí); 1100–1300 m ..... *P. fortunense* Croat

18b. Petioles glabrous, terete to merely obtusely flattened.

20a. Posterior rib naked along the sinus.

21a. Peduncle usually less than 10 cm long.

22a. Blades less than 25 cm long, the adaxial surface drying dark brown to yellow-brown.

23a. Blades ovate-triangular, 1.8–3 times longer than wide; posterior lobes 1.4–1.8

times longer than wide; inflorescence solitary; Panama (Chiriquí), 1750–2100 m ..... *P. knappiae* Croat

23b. Blades ovate, 1.3–1.6 times longer than wide; posterior lobes about as wide as long; inflorescences 2–3 per axil; Panama (Chiriquí), 1600 m ..... *P. coloradense* Croat

22b. Blades more than 35 cm long, the adaxial surface usually drying green to brownish green to grayish green to dark olive-green (sometimes dark brown in *P. zhuanum* or blackish in *P. smithii*).

24a. Petioles on drying not markedly flattened, 8–15 mm diam., usually greenish to dark brown; less than 360 m along the Caribbean coast in Costa Rica ..... *P. aromaticum* Croat & Grayum

24b. Petioles on drying markedly flattened, to 3–6 cm diam., often yellowish; 700–900 m, Coclé Province, Panama ..... *P. zhuanum* Croat

21b. Peduncle usually 10 or more cm long.

25a. Leaf blades with margins convex in lower ½ of blade.

26a. Stem drying light brown; epidermis often flaking; petioles spongiose, but drying moderately smooth, flattening to ca. 1 cm wide; blades drying thin and lacking conspicuous secretory canals; 40–1630 m (mostly less than 600 m), Mexico to Nicaragua ..... *P. smithii* Engl.

26b. Stem drying dark brown; epidermis sulcate or cracked but not flaking; petioles firm, drying heavily wrinkled, flattening to 3–6 cm wide; blades drying coriaceous with conspicuous secretory canals; 700–900 m, Panama (Coclé) ..... *P. zhuanum* Croat

25b. Blades with margins straight to concave in lower ½ of blade; Costa Rica and Panama.

27a. Leaf blades drying pale yellow-green, lacking any sign of secretory ducts on lower surface; ovules 1 per locule; Costa Rica, 1350–1400 m ..... *P. straminicaule* Croat

27b. Leaf blades drying dark olive-green or dark brown, with secretory ducts visible alternating with the minor veins on lower surface; ovules 4–5 per locule; near Costa Rican–Panamanian border, 1100–1950 m ..... *P. cotonense* Croat

20b. Posterior rib not naked along the sinus, or weakly and obscurely naked near its base.

28a. Blades with posterior lobes turned inward and overlapping; peduncles slender, drying ca. 2–4 mm diam.; 850–1560 m, Serranía de Pirre, Darién Province, Panama ... *P. clewellii* Croat

28a. Blades with posterior lobes never overlapping (except sometimes in *P. ferrugineum*), usually directed backward or somewhat outward; peduncles stout, usually 5–10 mm diam. on drying.

29a. Spathe barely or not at all constricted near the middle or above the tube portion; sterile staminate portion of the spadix often conspicuously (50%) broader than the pistillate portion at anthesis; Mexico to Guatemala, 70–2500 m ..... *P. advena* Schott

29b. Spathe usually visibly constricted above the tube (usually somewhat below the middle); sterile staminate portion of the spadix narrower to only slightly broader than the pistillate portion at anthesis.

30a. Inflorescences 1–3 per axil; spathes less than 11 cm long (except 9.5–18 cm long in *P. brenesii*).

31a. Primary lateral veins mostly more than 8 pairs; minor veins etched-sunken on upper blade surface; lower blade surface ± bluish green; 800–2200 m, Costa Rica and Panama ..... *P. brenesii* Standl.

31b. Primary lateral veins 4–8 pairs (sometimes to 9 pairs in *P. sagittifolium*); minor veins flat or raised on upper blade surface; lower blade surface medium green to yellow-green, not bluish green; Mexico and Belize.

32a. Leaf blades ca. 1.6 times longer than wide; ovules 1–7 per locule.

33a. Blades drying gray-green below; sap white; ovules 1 per locule; Belize, less than 500 m ..... *P. dwyeri* Croat

33b. Blades drying dark yellow-brown below; sap clear, turning brown?; ovules 4–7 per locule; Panama, 1600 m ..... *P. coloradense* Croat

32b. Leaf blades ca. 1.8–2 times longer than wide; ovules 2–4(5–8) or ca. 20 per locule; Mexico (Chiapas, 1300 m) or widespread, Mexico to South America, 150–2700 m.

34a. Blades ca. 1.8 times longer than wide; inflorescence 1 per axil; ovules 20 per locule; Mexico (Chiapas), 1300 m ..... *P. breedlovei* Croat

34b. Blades 1.85–2 times longer than wide, inflorescences 1–3 per axil; Mexico (Veracruz) to Colombia, 0–1800 m ..... *P. sagittifolium* Liebm.

30b. Inflorescences 4–6 per axil; spathes 15–23 cm long.

posterior lobes); posterior lobes 6.5–6.7 cm long, 7 cm wide, rounded; sinus obovate to narrow hippocrepiform and closed; midrib drying sunken and concolorous above, convex, matte below; basal veins 6 per side, with 2 free to base, third and higher order veins coalesced 1 cm, sunken above, convex below; posterior rib not naked; primary lateral veins 3 per side, departing midrib at a 40–45° angle, quilted-sunken above, round-raised or raised, darker below; minor veins distinct, arising from both the midrib and primary lateral veins; "cross-veins" prominently raised upon drying. INFLORESCENCES probably 1 per axil; peduncle 4.5 cm long, 4 mm diam., ± terete, glabrous; **spathe** 11 cm long (2.4 times longer than peduncle), green, drying dark reddish brown; **spadix** sessile, 9.5–10.5 cm long; pistillate portion 3 cm long, 1 cm diam.; staminate portion 6.5–7.5 cm long, 1–1.5 cm diam.; pistils 1.5 mm long, 1.9 mm diam.; ovary 6-locular, 1.2 mm diam., locules 1 mm long, 0.3 mm diam., ovule sac 0.1–0.2 mm long, with axile placentation; ovules ca. 14 per locule, 2-seriate, contained within small, cloudy, gelatinous ovule sac, 0.1–0.2 mm long, longer than funicle; funicle to 0.1 mm long, adnate to lower part of partition, style similar to style type B; style apex flat; stigma hemispheroid, lobed, 1 mm diam., 0.3–0.4 mm high, covering entire style apex, depressed shallowly at center; the androecium truncate, ± prismatic, margins irregularly 4–5-sided, ca. 1 mm long; sterile staminate flowers irregularly 4–5-sided, 1.6–2.1 mm long.

Flowering in *Philodendron hammelii* apparently occurs in the early wet season, based on a single collection made in June.

Philodendron hammelii is endemic to Panama, known only from the type in Coclé Province in *Premontane rain forest* at 850 to 1100 m elevation.

Philodendron hammelii is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is characterized by its short, slender internodes; persistent, thin, pale network of branched cataphyll fibers; petioles longer than the blades and densely covered with broad, pale scales near the apex; and ovate-cordate, yellow-green-drying blades.

Philodendron hammelii is superficially most similar to *P. colombianum* R. E. Schult. from the Amazon basin. These species have similarly shaped blades drying yellow-green with prominent "cross-veins" and persistent, pale cataphyll fibers. *Philodendron colombianum* differs, however, in having the blade sinus acute at apex and petioles lacking scales.

In Panama, this species might be confused with *P. squamipetiolatum,* which also has scaly petioles. It differs in having blades with a more arcuate sinus and petioles conspicuously long-scaly throughout most of their length.

The species is named in honor of Barry Hammel of the Missouri Botanical Garden who has collected many important Araceae in Panama and Costa Rica, including the type specimen.

Philodendron hebetatum Croat, sp. nov. TYPE: Panama. Coclé: vicinity el Valle de Antón, at forested flat area near Finca Macarenita at La Mesa, 800 m, 8°36′N, 80°07′W, 6 July 1994, *Croat & Zhu 76693* (holotype, MO–4619514–15; isotypes, B, CAS, COL, CR, F, K, NY, PMA, US). Figures 33, 218–220, 225, 226.

Planta hemiepiphytica; internodia 1–4 cm longa, 1.5–2.5 cm diam.; cataphylla ad 12–35 cm longa, incostata, persistentia semi-intacta; petiolus subteres, 27–75 cm longus, 0.8–1.8 cm diam., obtuse complanatus adaxialiter, in sicco conspicue flavibrunneus; lamina anguste ovato-triangularis, cordato-sagittata basi, 24–63 cm longa, 19–44 cm lata, atriviridi supra, opace albida, hebetata infra; inflorescentia 1–5; pedunculus 4–11 cm longus, 4–11 mm diam.; spatha 11–17.5 cm longa; lamina spathae extus viridi vel albida; tubo spathae extus atriviridi aut interdum purpureo vel violaceipurpureo vel rubro aut subroseo, intus albido vel rubello vel pallide violaceipurpureo; pistilla (4)5–8-locularia; loculi (4)20–24-ovulati.

Hemiepiphytic; stem appressed-climbing; internodes short, semiglossy, 1–4 cm long, 1.5–2.5 cm diam., longer than broad, green to gray-green, drying yellow-brown; roots moderately numerous per node, drying dark brown, ridged; cataphylls 12–35 cm long, unribbed, sometimes sharply 1-ribbed near apex (sharply 2-ribbed in South America), medium green, drying light to medium brown, persisting semi-intact at upper nodes, then deciduous with large patches of yellow-brown periderm remaining intact; **petioles** 27–75 cm long, 0.8–1.8 cm diam., ± terete, obtusely flattened adaxially, spongy (in South America), dark green to gray-green, surface semiglossy to matte, transversely fissured near apex, drying pale yellow-brown. LEAVES erect-spreading; **blades** ovate-triangular, subcoriaceous, abruptly acuminate at apex, cordate-sagittate at base, 24–63 cm long, 19–44 cm wide (1.1–2.3 times longer than wide), (0.7–1.2 times longer than petiole), equal to or longer than petiole, margins concave, broadly undulate, upper surface semiglossy, dark green, drying conspicuously yellow-brown, semiglossy, lower surface opaque whitish, matte, paler; anterior lobe 19.5–49.5 cm long, 14.5–42 cm wide (1.9–3.6 times longer than posterior lobes); posterior lobes 7.1–20.2

cm long, 7.3–20.5 cm wide, obtuse to rounded; midrib broadly concave, paler than surface above, thicker than broad, weakly glossy, darker than surface below; basal veins 6 per side, with 1–2 free to base, second and third veins coalesced ca. 3 cm; posterior rib naked for 2.5–3.5 cm long; primary lateral veins 6–11 per side, departing midrib at a 35–50° angle, weakly sunken above, convex and darker than surface below; minor veins moderately distinct, fine, intermittent below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1–5 per axil; peduncle 4–11 cm long, 4–11 mm diam., white-lineate to coarsely white-streaked toward apex and on spathe base; **spathe** 11–17.5 cm long, 2–3.5 cm diam. (1.3–3.1 times longer than peduncle), white-speckled, semiglossy, constricted above the tube, 9–11 mm diam. at constriction; spathe blade green to whitish, sometimes rose-red outside, green to whitish or sometimes rose-red and white-speckled inside; spathe tube oblong-ellipsoid, 4–7 cm long, usually dark green or sometimes purple to violet-purple to red or pinkish outside, reddish to pale violet-purple (dark maroon in South America) inside; **spadix** white, cylindrical, 12.9–16.6 cm long, broadest near the base, constricted near the middle; pistillate portion whitish, cylindrical to ovoid, 3.8–8.9 cm long, 7–16 mm diam.; staminate portion 9.3–13.4 cm long; fertile staminate portion cylindrical, 8–13 mm diam., broadest at the base, narrower than pistillate and sterile portions; sterile staminate portion as broad as or narrower than the pistillate portion, 1–1.3 cm diam.; pistils glossy, 2.1–4(5.8) mm long, 1.2–2.6 mm diam.; ovary (4)5–8-locular, walls embedded with granular, crystal-like particles, locules 1.3–3.2(4.5) mm long, 0.4–0.6 mm diam., with axile placentation; ovules (4)20–24 per locule, 2-seriate, 0.2 mm long, about equal in length to funicle; funicle 0.1 mm long, adnate to lower part of axillar wall, style 0.4–0.7 mm long, 1.2–2.6 mm diam., similar to style type B; style apex flat or rounded; stigma subdiscoid, 1–1.5 mm diam., 0.2–0.5 mm high, covering center of style apex; the androecium truncate, margins 4–6-sided, sometimes scalloped; thecae oblong, 0.3–0.4 mm wide, contiguous, ± parallel to one another; sterile staminate flowers 3–6-sided, 1.5–2.5 mm long, 1.4–1.8 mm wide. Berries white, with purple stigmas; seeds 2–3, 6, 10–12, 18–25 per locule, (1–5)8–11 mm long, 2–3 mm diam.

Flowering in *Philodendron hebetatum* apparently occurs throughout the dry season and first part of the rainy season in Panama, from December through July. Post-anthesis inflorescences have been collected from January through October (except September). Immature fruits have been collected in June and July. South American collections follow more or less the same pattern as those from Panama.

Philodendron hebetatum ranges from Panama to Colombia (Chocó) and Ecuador (Carchi, Esmeraldas, and Pichincha) along the Pacific coast, at 10 to 1880 m elevation in *Premontane wet forest, Tropical wet forest,* and *Premontane rain forest* life zones. It is to be expected in adjacent Costa Rica. In Panama, most collections have been made at or less than 1400 m, rarely to about 1630 m.

Philodendron hebetatum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Impolita.* This species is characterized by its generally appressed-climbing hemiepiphytic habit; short internodes; usually unribbed, semi-intact persistent cataphylls with large patches of yellow-brown epidermis remaining intact; petioles equaling or exceeding the blade in length and drying conspicuously yellow-brown and smooth (thus clearly demarcated from the blade); and markedly bicolorous, narrowly ovate-triangular blades usually concave along the margin and matte and whitish on the lower surface.

The petioles of *P. hebetatum* are variable, being typically terete to obtusely D-shaped in Central America but sharply C-shaped to sharply D-shaped with acute to bluntly raised lateral margins in South America. South American populations also have the major leaf veins drying yellowish to pale red vs. dark red in Central America. It is possible that the South American elements may ultimately prove to be at least subspecifically distinct.

Some South American specimens of *P. hebetatum* are particularly noteworthy. *Holm-Nielsen et al. 25665,* from Ecuador, differs from other collections in having the petiole epidermis drying paler yellow and the immature spathes drying a paler reddish brown. A collection from Nariño Department, Colombia (*Croat 72425A*), is unusual in having the margins of the anterior lobe markedly concave, but perhaps belongs also to this species.

Philodendron hebetatum is easily confused, especially in live condition, with *P. thalassicum,* which may also have triangular-ovate blades much paler and matte on the lower surface. The latter differs, however, in having petioles that are sharply D-shaped and dry blackened rather than conspicuously yellow-brown. In addition, *P. hebetatum* has spathes reddish within, while in *P. thalassicum* they are greenish within.

Philodendron hebetatum is also similar to *P. strictum,* which differs by its usually terrestrial hab-

it, more or less reclining stems, and broadly ovate blades. Both species have pale, matte lower blade surfaces, yellow-brown drying petioles, and cataphylls with persistent patches of intact, yellowish brown epidermis. The lower blade surface in both species is covered with a wax-like substance, and dries with a fine reticulate pattern (areolate at 7× or higher magnification). *Philodendron strictum* ranges from Costa Rica to Panama and Venezuela at 650 to 1900 m elevation. In Panama, where both species occur together along the Fortuna Dam Road, *P. strictum* tends to occur at higher elevations than *P. hebetatum.*

Juvenile plants (*Croat 56049, 56174, 56213, 69291*; Valle and Chocó Departments, Colombia) of *P. hebetatum* have oblong-elliptic leaf blades acute at the base, but the petiolar epidermis already is colored as in adult plants. Leaves of older plants become increasingly rounder and broader at the base and finally subcordate to cordate.

An unusual collection is *Croat 49298* from Chocó Department, Colombia, with leaves only shallowly cordate, even though they are in the upper end of the size range for adult plants of this species.

Sánchez et al. 553, a collection from Colombia (Antioquia), is noteworthy in being from 1880 m elevation and in being terrestrial. *Holm-Nielsen et al. 25665* from Ecuador (Esmeraldas) differs from other South American collections in having a paler, flakier epidermis on the petioles and smaller, more or less sessile (perhaps immature) inflorescences. Perhaps it represents another species. South American collections of *P. hebetatum* differ from those of Panamanian material in that the petioles dry dark brown rather than yellowish.

Croat 61396 is unusual in apparently having only four ovules per locule.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 2.8 mi. N of Divide, 850–950 m, ca. 8°45′N, 82°15′W, *McPherson 9663* (MO, NY); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60263* (CM, MO); 13.2 mi. W of Chiriquí Grande, 310 m, 8°45′N, 82°10′W, *60140* (AAU, MO). **Chiriquí**: Cerro Colorado, 18–27 mi. off Pan-American Highway along mining road, 1200–1500 m, *Croat 33141* (MO); 1390–1410 m, *Croat 37223* (MO); 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69064* (CM, MO, PMA); 8.3 mi. beyond Chame, 1630 m, *Croat 75042* (MO); *75046* (CM, MO); Fortuna Dam area, 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°07′W, *Croat & Grayum 60073* (B, CM, MO); 11.8 mi. N of Los Planes de Hornito, *Croat 48668* (MO). **Coclé**: El Copé region, 9.4 km above El Copé, 750–900 m, *Croat 44686* (CAS, MO); Alto Calvario, 800 m, 8°39′N, 80°36′W, *Croat 75075* (CM, MO); 710–800 m, 8°39′N, 80°36′W, *Croat 68712* (ENCB, MO); El Valle region, vic. of La Mesa, N of El Valle de Antón, 900–1000 m, 8°37′N, 80°08′W, *Croat 67279* (MO); 8°37′N, 80°07′W, *McPherson 11203* (CM, M, MO); 8°40′N, 80°07′W, *Knapp 5337* (MO); *5753* (MEXU, MO); La Mesa, 775 m, 8°36′N, 80°07′W, *Croat 74783* (MO, QCA); *14372* (MO); 2000–2700 ft., *Dwyer et al. 4567* (MO, NY); 860–900 m, *Croat 37364* (MO); ca. 800 m, *25407* (MO); 800–900 m, 8°38′N, 80°09′W, *67204* (DUKE, MO, US). **Darién**: Parque Nacional Darién, near gold mine at headwaters of N branch of Río Pucuro, slopes of Cerro Tacarcuna, ca. 6 km N of Cerro Mali, 1300–1500 m, 8°09′5″N, 77°15′W, *Hammel et al. 16541* (COL, MO); Río Tuquesa, Tyler Kittredge gold mine, ca. 2 air km from Continental Divide, *Croat 27240* (MO). **Panamá**: Cerro Jefe region, vic. of summit, 850 m, 9°14′N, 79°22′W, *Croat 67060* (MO, NY); 0.8 mi. beyond turnoff to Altos de Pacora, 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76611* (CM, K, M, MEXU, MO, W); 4.6 km beyond peak on road to Alto de Pacora, 26.3 km from InterAmerican Highway, 600 m, *Croat 35934* (MO); 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above highway, 700–750 m, 9°15′N, 79°25′W, *Croat 68661* (IBE, MO); 5–10 km NE of Altos de Pacora, 700–800 m, *Mori & Kallunki 6031* (MO); El Llano–Cartí Road, Mile 10, near El Llano, 330 m, *Croat 33773* (MO, US); Cerro Campana, ca. 850 m, 8°40′N, 79°50′W, *Thompson 4598* (MO), *Croat 17243* (MO), 780–875 m, *25224* (F, MO, PMA); 1000 m, *Luteyn 3193* (DUKE); ca. 1 mi. from Inter-American Highway, ca. 150 m, *Croat 35961* (F, MO); above Su Lin Motel, *Croat 14726* (MO, PMA); lower slopes above FSU cabin, 850 m, *Croat 22795A* (MO). **San Blas**: El Llano–Cartí Road, Mile 14, 300 m, 9°15′N, 79°W, *Croat 69231* (MO, PMA, SAR); sendero de Interpretación, 1 km al este del Campamento de los guardabosques de INRENARE, 800–900 m, 8°40′N, 79°55′W, *Correa et al. 9489* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río Calovébora, 0.6 mi. beyond Escuela Agrícola Alto Piedra, 735 m, *Croat & Folsom 33996* (MO); Cerro Tute, 800–1100 m, 8°35′N, 81°5′W, *Hamilton & Krager 3934* (MO); Río Tercero Braso Valley, beyond Escuela Agrícola Alto Piedra, above Santa Fe, *Croat 27326* (MO).

COLOMBIA. **Antioquia**: Mpio. Frontino, Corregiento Nutibara, valley of the upper Río Cuevas, 1880 m, *Sánchez et al. 553* (MEDEL); Río Anorí, confluence of Quebrada La Tirana and Río Anorí, ca. 3 km upriver from Planta Providencia, 28 km SW of Zaragoza, 400–700 m, *Alverson et al. 299* (COL, WIS); Río Anorí valley near Planta Providencia, 350–600 m, 7°30′N, 74°50′W, *Shepherd 924* (COL, WIS). **Chocó**: Quibdó–Tutunendo Road, ca. 3 km W of Tutunendo, 80 m, *Gentry et al. 30108* (MO); 1 km E of Tutunendo, 100 m, 5°46′N, 76°35′W, *Gentry et al. 30079* (COL); Medellín–Quibdó, Km 136.4, 63 km E of Tutunendo, 960 m, 5°47′N, 76°22′W, *Croat 56348* (COL, JAUM, MO); Km 208.5, 9 km W of Tutunedo, <100 m, 5°39′N, 76°40′W, *Croat 56213* (MO); Río Atrato, 39 km W of Bolívar, 1600 m, *Croat 49261* (MO); 78 km W of Bolívar, 466 m, *Croat 49298* (MO); 27 mi. W of Bolívar, 1190 m, 5°50′N, 76°16′W, *Croat & Cogollo 52089* (MO); Quibdó–Bolívar, Km 137–138, 79–80 km E of Quibdó, 910–920 m, 5°45′N, 76°21′30″W, *Croat 57345* (COL, JAUM, MO); Quibdó-Las Animas, ca. 1 km N of Las Animas, ca. 100 m, 5°14′N, 76°40′W, *Croat 55958* (COL, MO); San José del Palmar–Cartago, Vereda La Bella between San José del Palmar and turnoff to El Cairo, 1430 m, 4°53′N, 76°13′W, *Croat 56715* (COL, MO, QCA); Pueblo Rico (Risaralda)–Istmina (Chocó), Quebrada Antón, 15 km W of Santa Cecilia, 6 km W of Chocó–Risaralda border, 240–350 m, 5°20′30″N, 76°13′45″W, *Croat 70961* (MO); Quibdó–Istmina, Km 4, <100 m, 6°28′N,

76°36′W, *Croat & Cogollo 52234* (MO); Serranía de Baudo, Las Animas–Pato on Río Pato, ca. 150 m, 5°30′N, 76°46′W, *Croat 56131* (COL, JAUM, MO, PMA); 16 km NW of junction with Quibdó–Istmina road near Las Animas, 100 m, 5°20′N, 76°42′W, *Croat 56174* (COL, JAUM, MO); 5°16′N, 76°41′W, *Croat 56049* (COL, JAUM, MO); Río San Juan, Docordó, 0 m, 4°15′N, 77°22′W, *Forero et al. 4352* (MO). **Nariño**: along road between Junín and Barbacoas, 1.9 km NE of Junín, 1130 m, 1°21′N, 87°6′W, *Croat 72425A* (CM, MO). **Risaralda**: Mpio. Mistrato, Chirrincha, Río Aguita, 950 m, *Franco et al. 3522* (MO); corregimientos de Geguadas–Puerto de Oro, 1550 m, *Alonso et al. 9819* (MO); *9742* (MO). **Valle**: Bajo Calima area, *Croat 62761* (CM, MO); ca. 15 km N of Buenaventura, Cartón de Colombia concession, Juanchaco region, 500 m, 3°56′N, 77°08′W, *Gentry et al. 53711* (MO); Lijal–Gasolina road junction, SSW of San Isidro, 50 m, *Gentry et al. 62926* (MO); 11 km N of main Cali–Buenaventura Highway, ca. 50 m, 3°56′30″N, 77°01′W, *Croat & Monsalve 61396* (MO, QCA); Buenaventura–Río Calima, 33.3 km N of Cali–Buenaventura Highway, ca. 50 m, 4°02′N, 77°07′W, *Croat 61279* (COL, MO, NY, TEX); Km 11, 50–80 m, 3°56′30″N, 77°01′W, *Croat 69291* (CAS, F, L, MO, US); ca. 4 km from Río Calima, near Km 14 marker, <50 m, 3°56′N, 76°59′W, *Croat 57530* (AAU, DUKE, K, MEXU, MO); Buenaventura–Málaga Road, 185 m, 3°56′N, 77°01′W, *Croat 70103* (B, CAS, COL, F, K, MO, PMA, US); km 17.5, 130 m, 3°57′N, 77°01′W, *Croat & Bay 75629* (MO); Km 18–20 on Cali–Buenaventura Highway, Finca Zingara, 1500–2000 m, *Cabrera & van der Werff 15779* (MO); Río Cajambre, 5–80 m, *Cuatrecasas 17054* (US); Río Naya, upriver from Puerto Merizalde, ca. 10 m, 3°15′N, 77°25′W, *Gentry & Juncosa 40673* (MO). ECUADOR. **Carchi**: Tulcán Cantón, Reserva Indígena Awá, sector Sabalera, parroquia Tobar Donoso, 650–100 m, 1°N, 78°24′W, *Tipaz et al. 1298* (MO); *1462* (MO). **Esmeraldas**: Lita–San Lorenzo, 15.5 km W of Lita, 705 m, 0°55′N, 78°28′W, *Croat 72372* (MO); San José de Cayapas, 80 m, 0°52′N, 78°57′W, *Holm-Nielsen et al. 25665* (AAU, MO); Eloy Alfaro, Reserva Ecológica Cotacachi–Cayapas, Charco Vicente, Río San Miguel, afluente del Río Cayapas, 150 m, 0°43′N, 78°53′W, *Palacios & Tirado 11276* (MO, QCNE). **Pichincha**: Reserva ENDESA, Quito–Puerto Quito, Km 113, 0°05′N, 79°02′W, 750 m, *Croat & Rodríguez 61454* (CM, K, M, MO, QCA); *61455* (K, MO, QCA); 710 m, 0°03′N, 79°07′W, *Croat 73155* (AAU, B, COL, F, K, MO, NY, QCA, US).

Philodendron hederaceum (Jacq.) Schott, Wiener Z. Kunst. 1829: 780. 1829. *Arum hederaceum* Jacq., Enum. Syst. Pl. 31. 1760. TYPE: t. 51, fig. D in Plum., Pl. Amer., 1756 (holotype). Figures 221–223.

Hemiepiphytic vine; growing to often high in trees, stem appressed-climbing, eventually scandent, often pendent, sap clear, turning honey-colored, leaf scars 7–15 mm long; internodes weakly flattened on one side, sometimes with 2 sharply raised on the side above the petioles, usually weakly glossy, sometimes matte, pale to medium green, minutely speckled to striate, usually smooth when fresh, but drying minutely ridged, sometimes prominently ribbed throughout its circumference (the ribs smooth to prominently warty), (2)10–28 cm long, 1–2.5(3.5) cm diam., dark green, usually drying green, sometimes reddish; roots brown, to 10 cm long, many at nodes; cataphylls 6–10 cm long, unribbed, weakly 1-ribbed, or bluntly to sharply 2-ribbed, pale green, deciduous; **petioles** (6)9.7–27(33) cm long, 6–10 mm diam., terete to subterete, pale green, firm, flattened adaxially, pale green, surface smooth, weakly glossy to matte; **blades** broadly ovate, subcoriaceous to coriaceous, semiglossy to matte, acuminate to long acuminate, sometimes cuspidate at apex (the acumen inrolled, 0.5–0.9 mm long), 11–40(50) cm long, 8–24(34) cm wide (1.2–1.9 times longer than wide), (ca. 1.3(1.5) times longer than petiole), margins hyaline to pale yellowish, upper surface dark green, sometimes subvelvety, lower surface slightly paler, often purplish violet, drying gray-green to yellow-green; anterior lobe 9–30(41) cm long, 9–24(29) cm wide ((2)2.4–3.7(6.3) times longer than posterior lobes); posterior lobes 3–10(14) cm long, 4.3–15.7 cm wide, directed inward and sometimes overlapped, obtuse to rounded; sinus usually deeper than broad, mostly spathulate, rarely hippocrepiform, 3–7 cm deep; midrib convex to flat or sunken, concolorous or slightly paler than surface above, convex, concolorous below; basal veins (3)4–5(6) per side, with (0)1–2 free to base, part of the remainder coalesced to 1.5–2 cm; posterior rib not naked; primary lateral veins 2–6 per side, departing midrib at a 35–55° angle, ± straight to the margins, sunken to weakly raised, slightly paler than surface above, convex and paler than surface below; minor veins obscured to moderately distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES erect or pendent, 1 per axil; peduncle (2–3)4–15.7 cm long, 8–12 mm diam., pale green, sometimes tinged purple, matte; **spathe** subcoriaceous to coriaceous, 9–16.6(24) cm long, (0.9–2.6(3.3) times longer than peduncle), weakly constricted above the tube, 1.3–3.6(5.7) cm diam. at constriction, usually green, sometimes yellowish white, yellowish green, or cream to creamy-white throughout; spathe blade sometimes purple tinged outside, 1.2–3.6 cm diam. when furled, pale green, greenish yellow, sometimes tinged red inside; spathe tube dark green, sometimes tinged reddish maroon outside, 5–6 cm long, 1.5–4.9(6.9) cm diam., maroon, dark red, crimson, or purple at base inside; **spadix** stipitate to 5–10 mm long, dark maroon; 12–20 cm long; pistillate portion pale greenish white to green, 3.5–6 cm long, 1.5 cm diam. at base, 1.7 cm diam. at middle and near apex; staminate portion 7–11 cm long; fertile staminate portion creamy white to pinkish, broadest at base,

weakly constricted ca. 1 cm above sterile portion then ± uniform to near apex, 1.4–2.2 cm diam. at middle, 9 mm diam. ca. 1 cm from apex; sterile staminate portion 1.6 cm diam.; pistils 4–9.2 mm long, 1.8–3.1 mm diam.; ovary 4–6(7)-locular, 8 mm long, locules 8 mm long, 1.4 mm diam., with axile placentation; ovules 20–25 per locule, 0.1 mm long, 2-seriate; funicle 0.1–0.3 mm long, adnate to lower part of partition, style 1.1 mm long, 2.9 mm diam., similar to style type B; style apex flat or somewhat rounded, drying concave with a pale margin and 4–6 paler, flat to weakly sunken circular areas associated with the stylar pores; stigma 3–4-sided, light brown to reddish, drying light brown, 1.8–3.3 mm diam., 0.35 mm high, margins thin; sterile staminate flowers blunt, irregularly 4–5-sided, 2.2 mm long, 1.3 mm wide. INFRUCTESCENCE pendent, often on leafless stems; spathe dark green, weakly glossy outside; pistillate spadix 5–8 cm long, 3.5–4 cm diam.; berries greenish white; seeds 1–2 per locule, somewhat orange, many per berry, ± ovoid to oblong ellipsoid, (1.5)3–5 mm long, 2.5–4 mm diam., with weak constriction (nipple) and densely covered with raphide cells. JUVENILE plants with upper blade surface dark green, sometimes reddish green, with glistening minute close papillations, lower surface somewhat maroon; veins less conspicuous.

Philodendron hederaceum ranges throughout the West Indies and from Mexico throughout Central America and much of South America, at sea level to 1200(1500) m elevation. In South America it extends from as far south as Los Ríos Province in coastal Ecuador to Trinidad, Venezuela, the Guianas, Brazil, Ecuador, Peru, and Bolivia on the Atlantic drainage of the continent.

Philodendron hederaceum is a member of *P.* sect. *Philodendron* subsect. *Solenosterigma.* This species is distinguished by its scandent habit, long internodes, deciduous cataphylls, ovate-cordate, long-petiolate leaves, and solitary inflorescence with usually green spathes with the tube reddish to purplish within.

Philodendron hederaceum is most easily confused with *P. purpureoviride,* which is a vine with similar leaves. See that species for differences.

Philodendron hederaceum is also somewhat similar to *P. jacquinii,* but the latter differs in its generally pubescent stems, petioles and major veins of the lower blade surface, its thinner leaf blades, swollen spathe tube, and broad pistillate portion of the spadix with elongate styles.

The taxa here treated as *Philodendron hederaceum* and *P. jacquinii* have long been confused nomenclaturally. The former name is based on *Arum hederaceum,* first validly published by N. J. Jacquin (1760) in his *Enumeratio Systematica Plantarum.* Jacquin cited only a Plumier (1756) plate (t. 51, fig. d), which thus must be accepted as the holotype of the name (Greuter et al., 1994; Art. 9.1, Note 1). Three years later, Jacquin (1763), in his *Selectarum Stirpium Americanarum Historia,* published his own plate (t. 152), identified as *A. hederaceum* but actually depicting a different species from Cartagena, Colombia, namely, that treated in this revision as *P. jacquinii* Schott. These two species are fortunately sufficiently different in appearance that even drawings of sterile plants, such as that of Plumier, are unmistakable. This mistake by Jacquin has caused considerable confusion, since several authors, including Kunth (1841), Engler (1899), Krause (1913), Dugand (1945), and Bunting (1963b, 1995), have misapplied the name *P. hederaceum* based on Jacquin's (1763) publication.

Schott, however, understood the problem. He had already transferred *Arum hederaceum* to *Philodendron* (Schott, 1829), and in his treatment for *Synopsis Aroidearum* (Schott, 1856) he described *P. jacquinii,* explicitly basing it on Jacquin's (1763) plate. Schott (1856) also placed *P. hederaceum* sensu Kunth into synonymy under his newly described *P. jacquinii.* However, he included *P. hederaceum* in his grex *Macrobelium,* while treating other synonyms of *P. hederaceum* in grex *Solenosterigma.* Names so treated were: *P. scandens, P. prieurianum, P. oxycardium, P. cuspidatum,* and *P. micans.*

Engler (1899), followed by Krause (1913), treated the species herein called *P. hederaceum* as four distinct species: *P. prieurianum, P. scandens, P. oxycardium,* and *P. micans.* Both Engler and Krause erred in treating *Arum hederaceum* Jacq. as a questionable synonym of *P. hoffmannii* (= *P. jacquinii*), citing Jacquin's (1763) t. 152 as the type.

Despite the confusion by Engler and Krause, Standley and Steyermark (1958b) correctly dealt with the taxonomy of *P. hederaceum,* citing *P. scandens, P. oxycardium,* and *P. miduhoi* in synonymy. Their treatment of *P. jacquinii* was incorrect, since they cited that name under the later synonym *P. hoffmannii* Schott (1858). In this regard they followed Krause (1913). Thus, despite the confusion by Engler and by Krause, the nomenclature of these species was essentially rectified as early as 1958 to the species as *P. oxycardium* or *P. cordatum* hort. (non Vell.).

Bunting (1963b), apparently following the lead of Dugand (1945), was aware of the Plumier illustration cited by Jacquin but seemed to believe that it had no bearing on the application of the name.

He also referred to Jacquin (1763) as the "initial" publication of *Arum hederaceum*, presumably in the erroneous belief that the name had not been validly published in Jacquin (1760). Bunting (1963a) accordingly applied the name *P. hederaceum* to the species here called *P. jacquinii* and the obscure *P. scandens* K. Koch (1853) for the species herein called *P. hederaceum*. Certainly the epithet *P. scandens* was not in general use up until that time because most horticultural works (Birdsey, 1951) still referred to the species as *P. oxycardium* Schott.

Other, more practical matters substantiate that Plumier's (1756) rather crude drawing depicts the species here treated as *P. hederaceum*, rather than the one called *P. jacquinii* (accurately illustrated by Jacquin, 1763). Plumier's text associated with t. 51, fig. D states that the plant grew in Martinique, known to have been visited by Plumier (Urban, 1898: 123). *Philodendron hederaceum* is a widespread species in the West Indies and occurs on Martinique, while *P. jacquinii*, though also widespread, is not known from the Lesser Antilles. The epithet *hederaceum* connotes an ivy-like growth habit and aspect, apt for the species to which the epithet is here applied, but not for *P. jacquinii*. The application of the name *P. hederaceum*, as explained above, is unambiguous, whereas that of *P. scandens*, the name used during the last 30 years for this plant, is highly dubious, as it is based on a sterile Koch specimen of unknown origin, lacking an extant type specimen or even illustrations.

Article 57.1 of the Tokyo Code (Greuter et al., 1994) states that "A name that has been widely and persistently used for a taxon or taxa not including its type is not to be used in a sense that conflicts with current usage unless and until a proposal to deal with it under Art. 14.1 or 56.1 has been submitted and rejected." I consider that this Article does not apply in the present case, since the name *P. hederaceum* was used in the sense, including its type, as recently as 1958, in a higher regional flora (*Flora of Guatemala*), which is the most recently published treatment of Araceae for any Central American country and still reigns as the standard work throughout the region.

In Central America, *P. hederaceum* can be divided into three varieties. *Philodendron hederaceum* var. *hederaceum* and *P. hederaceum* var. *oxycardium* (Schott) Croat are only distinguishable on the basis of their juvenile leaf blades. In *P. hederaceum* var. *hederaceum*, the juvenile blades are velvety with a silky sheen on the upper surface, whereas the juvenile blades of *P. hederaceum* var. *oxycardium* are glossy on the upper surface. These juvenile forms were formally treated by Bunting (1968) as *P. scandens* forma *micans*.

The third newly recognized variety, *P. hederaceum* var. *kirkbridei* Croat, is distinguishable by its adult stems that dry brown and are deeply sulcate with prominent ridges. This taxon also differs in occurring at higher elevations.

The following key separates the three varieties of *P. hederaceum* in Central America. For anatomical differences see Bunting (1968).

KEY TO THE VARIETIES OF *P. HEDERACEUM*

1a. Adult stems weakly sulcate on living plants, moderately to conspicuously sulcate and reddish brown upon drying, usually densely warty; spathe tube dark red to red-purple inside; Costa Rica, Panama, Ecuador, and Suriname, mostly 450–900 m elevation ..... var. *kirkbridei*

1b. Adult stems smooth, drying mostly green, weakly striate, never minutely warty; spathe tube green (sometimes weakly tinged reddish) inside.

2a. Juvenile blades velvety with a lustrous sheen on the upper surface, often tinged purplish on the lower surface; apparently ranging throughout the range of the species in Mexico, Central America, and to the West Indies and South America (including Amazonian basin) ..... var. *hederaceum*

2b. Juvenile blades glossy on the upper surface, green on the lower surface; known only from the Gulf slope of Mexico in Veracruz, northern Oaxaca, and Tabasco, but possibly also found in Jamaica ..... var. *oxycardium*

Philodendron hederaceum (Jacq.) Schott var. **hederaceum**

Philodendron scandens K. Koch & Sello, in A. Braun et al., Append. sp. Hort. berol. 1853: 14. 1853–1854. TYPE: A cultivated plant grown in Berlin, origin not stated (holotype, B lost).

Philodendron harlowii I. M. Johnst., Sargentia 8: 91, t. 14, fig. 1. 1949. TYPE: Panama. Panamá: San José Island, area 11B, *Johnston 1030* (holotype, GH; isotype, MO).

Philodendron miduhoi Matuda, Revista Soc. Mex. Hist. Nat. 11: 95, figs. 6–7. 1950. TYPE: Mexico. Chiapas: Finca Esperanza, 160 m, 23 Dec. 1949, *Matuda 18721* (holotype, MEXU; isotype, UC).

Philodendron cuspidatum K. Koch & Bouché, in A. Braun et al., Append. Gen. sp. Hort. berol. 1854: 7. 1854–1850. *Philodendron scandens* var. *cuspidatum* (K. Koch & Bouché) Engl., Bot. Jahrb. Syst. 26: 528. 1899. TYPE: cultivated at Berlin Botanical Garden (holotype, B? destroyed). Schott ic. 2679 (neotype, here designated).

Philodendron micans K. Koch, in A. Braun et al., Append. Gen. sp. Hort. berol. 1854: 7. 1854–1855. *Philodendron scandens* f. *micans* (K. Koch) G. S. Bunting, Gentes Herb. 10: 63. 1968. TYPE: original locality unknown (holotype, B? destroyed). Schott ic. 2709 (neotype, here designated, W).

Philodendron microphyllum K. Koch, in A. Braun et al., Append. Gen. sp. Hort. berol. 1854: 7. 1854–1855. TYPE: cultivated collection at Berlin (holotype, B? now lost).

Philodendron oxyprorum Schott, Syn. Aroid. 82. 1856. TYPE: Venezuela. [Synonymized by Engler (1899) but no specimen or illustration now exists.]

Philodendron acrocardium Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: Guatemala, *Wendland* (holotype, W? destroyed). Schott ic. 2498 (neotype, here designated).

Philodendron pittieri Engl., Bot. Jahrb. Syst. 26: 541. 1899. TYPE: Costa Rica. Puntarenas: Ujarrás de Buenos Aires, 9°12′N, 83°17′W, Feb. 1897, *Pittier 11132* (holotype, B; isotype, BR).

Hemiepiphyte; internodes 10–25 cm long, 1–2.5(3.5) cm diam., weakly flattened on one side, medium green, minutely speckled to striate or smooth when fresh but drying minutely ridged, greenish; cataphylls 6–10 cm long, unribbed, weakly 1-ribbed or bluntly to sharply 2-ribbed, deciduous intact; **petioles** (6)10–27(33) cm long, 6–10 mm diam.; blades (11)16–40(50) cm long, 8–24(34) cm wide; upper surface medium to dark green, velvety when juvenile, drying brown to greenish brown, lower surface medium green, glossy, drying gray-green to yellow-green; primary lateral veins 2–6 per side, departing midrib at a 35–55° angle. INFLORESCENCES with peduncle (2)4–16 cm long; **spathe** 9–17(20) cm long, spathe usually green, sometimes yellowish white, spathe blade sometimes tinged purple outside; spathe tube dark, sometimes tinged reddish maroon outside; **spadix** stipitate to 5 mm, 12–18 cm long; ovary 4–6-locular, 20–25 ovules per locule. INFRUCTESCENCES with many seeds per locule.

Flowering in *Philodendron hederaceum* var. *hederaceum* is rare (known only in October and November), although the species has been found in pre-anthesis condition in every month of the year. Post-anthesis collections predominate in the dry season and earliest part of the rainy season from December through May, but there are a surprisingly large number of post-anthesis collections made in November, a month when very little flowering generally takes place (Croat, 1975, 1978). Mature fruiting collections have been made from April and May, also indicating that the species may flower predominantly in the dry season.

The range of *P. hederaceum* var. *hederaceum* is essentially that of the species. It is the most widespread taxon of *Philodendron* and, indeed, perhaps of all neotropical Araceae, ranging from San Luis Potosí State in Mexico to the Greater and Lesser Antilles, and down both slopes of the Andes, east to the Guianas and south to Brazil and Bolivia. In Central America, the variety occurs on both slopes of the Continental Divide. In Mexico, it ranges from sea level to 1200(1500) m elevation, whereas in Middle America and Panama it ranges mostly to 450 (rarely to 900) m. It occurs principally in *Tropical moist forest* but ranges into *Premontane wet forest* and even *Tropical wet forest.* A single sterile pre-adult collection from *Tropical wet forest* transition to *Premontane wet forest* in Bajo Calima (*Bay 237*) is apparently also this species.

Additional specimens examined for P. hederaceum *var.* hederaceum. BELIZE. *Gentle 617A* (MICH). **Cayo**: S of Guacamallo Bridge, *Whitefoord 2837* (BM); Millionario–Grano de Oro, 1700 ft., *Croat 23697* (MO); 0–10 mi. S on Hummingbird Highway, Belmopan, *Dwyer 12718* (MO); Río Frío, 1.5 mi. W of Augustine, 450 m, *Sutton et al. 205* (BM); 0.9 km before Caracol, 16°46′N, 89°07′W, *Balick et al. 3149* (MO). **Stann Creek**: Cockscomb Basin, Jaguar Preserve, 10 km W of Maya Center, off Southern Highway, 400 m, 16°45′N, 88°35′W, *Balick et al. 2603* (MO). **Toledo**: along highway to Punta Gorda, 1 mi. E of road to San Antonio, ca. 100 ft., *Croat 24511* (MO); Union Camp, 750 m, *Whitefoord 1773* (BM, MO); Columbia River Forest Reserve, Gloria Camp, *Holst 4422* (MO); Southern Maya Mountains, Bladen Nature Reserve, 16°29′31″N, 88°54′37″W, *Davidse & Meadows 35763* (MO). COSTA RICA. *Monell s.n.* (MO); *Tonduz 13322* (G); 800 m, *Rojas 178* (MO). **Alajuela**: Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36320* (MO); Escuela Centroameriana de Ganadería, (near Atenas), 425 m, 9°58′N, 84°22′W, *Thompson & Rawlins 1256* (CM). **Guanacaste**: Tilarán, 500–650 m, *Standley & Valerio 44563* (US); *44162* (US); *44984* (US); *46563* (US); 7 km N of Cañas, *Janzen T-24* (MO); Quebrada Desprendimiento–Quebrada Sanguijuela, along Río Las Flores, ca. 450 m, 10°40′N, 85°04′5″W, *Grayum et al. 4912* (B, CAS, CR, K, MO, US); Nandayure, Península de Nicoya, 120 m, *A. Rodriguez & Estrada 141* (CR, INB). **Heredia**: La Selva Field Station, ca. 100 m, *McDowell 810* (MO); ca. 100 m; *852* (MO); *Grayum 2565* (MO). **Limón**: 20 mi. SE of Limón, road to Punta Cahiuta, near sea level, *Croat 43174* (MO); ca. 1 km N of Shiroles, ca. 50 m, *Croat 43278* (MO); Siquirres–Río Pacuare, S of Río Pacuare, 50–100 m, 10°5′N, 83°29′W, *Burger & Liesner 6953* (MO, NY); La Bomba–Cahuita, 20 m, *Gómez & Hampshire 20129* (MO); Limón–Bomba, 0–50 m, *Taylor & Skotak 4443* (DUKE); near Carmen Station on Indiana Branch, 30 m, *Standley & Valerio 48392* (US); Parque Nacional Bahía de Portete, 0–10 m, 10°N, 83°05′W, *Thompson & Rawlins 1178* (CM); Río Jiménez, S of Guápiles, 10°17′N, 83°44′W, *Barringer 2393* (CR, MO). **Puntarenas**: Cantón de Buenos Aires, along Río Ceibo, Ujarrás, 500 m, 9°14′N, 83°18′W, *Grayum 10229* (CR, IBN, K, MO, US); Golfito, 20–200 m, 8°38′N, 83°11′15″W, *H. Schmidt 603* (CR, MO); San Vito, *Benzecry CR.CB.7C.109* (CR); Monteverde, Cordillera de Tilarán, 1500–1620 m, *Pounds 94* (MO); Cantón de Turrubares, along Río del Sur, between Río Carara and Quebrada Cimarruda, 130–150 m, 9°46′30″N, 84°32′W, *Grayum 10420* (CR, MO). EL SALVADOR. **Ahuachapán**: San Francisco Menéndez–Tacuba, 1–3 mi. above road to Río Clara Sucia, 1000–1250 m, *Croat 42135* (MO). **San Miguel**: ca. 50 mi. NW of San Miguel, along highway CA-1, *Croat 32799* (MO). **San Salvador**: vic. of Tonacatepeque, *Standley 19533* (GH, NY, US). **Sonsonate**:

Pedregal de San Isidro, ca. 3 mi. S of Lake Coatepeque, ca. 850 m, *Croat 42241* (MO). GUATEMALA. Los Amates, *Kellerman s.n.* (US); *Watson 427* (GH). **Alta Verapaz**: road to El Estor (Lago Izabal), 7 mi. E of Highway CA-14 to Cobán, 1000 m, *Croat 41480* (MO). **Escuintla**: Santa Lucia, 1045 ft., *Kellerman 4547* (US); *5285* (US). **Izabal**: Montaña del Mico, between Milla 49.5 and ridge 6 mi. from Izabal, 65–600 m, *Steyermark 38486* (F); ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41811* (MO). **Quezaltenango**: CA-2 between Coatepeque and turnoff to Colombia, 1.9 mi. W of turnoff, 580 m, 14°41′N, 91°48′W, *Croat 63394* (B, BM, MO, US). **San Marcos**: near San Rafael, 600 m, *Croat 40769* (MO). **Suchitepéquez**: 1 mi. E of Mazatenango, <500 m, *Croat 43757* (MO). HONDURAS. **Atlántida**: Lancetilla Valley, Tonacatepeque, *Pfeifer 2130* (BH, US); San José de Texíguat–El Chorizo, 100 m, *Nelson 10565* (TEFH); 4 km S of Tela, 0–100 m, *Irias 190* (TEFH, UNAH); ca. 10 mi. SE of Tela, along Río Lancetilla, 10–150 m, *Croat 42639* (MO); Quebrada Grande, ca. 10 km SW of La Ceiba, 80–140 m, 15°42′N, 86°51′W, *Liesner 26335* (MO). **Colón**: Río Selen, 7 km E of Trujillo, Howler Site, *Saunders 192* (MO). **Comayagua**: junction Río Yure–Río Humuya, 200 m, *Nelson et al. 6182* (MO). **Copán**: 13 mi. E of Copán, road to La Entrada, 750 m, *Croat 42529* (MO); Sta. Rita village, 650 m, *Molina 33668* (MO). **Cortés**: Puerto Cortés–Guatemalan border, 2–3 mi. SW of Omoa, sea level, *Croat 42555* (MO); N of Lago de Yojoa, 2–6 mi. from highway, 600 m, *Croat 42739* (MO). **Gracias a Dios**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9316* (UNAH); *9292* (TEFH, UNAH). **Olancho**: Mpio. San Estebán, near Santa María del Carbón, 21 mi. NE of San Estebán, along road to Bonito Oriental, 440 m, 15°25′25″N, 85°34′45″W, *Davidse et al. 35571* (MO; Río Guyape, San Pedro de Catacamas–Poncaya, *Blackmore & Heath 1984* (BM); Río Wampú, 8 km S of Pisijire, 500–700 m, 15°15′N, 85°25′W, *Nelson & Clewell 594* (FSU, MO). MEXICO. **Chiapas**: El Triunfo, ca. 10 mi. NE of Escuintla, 300 m, *Croat 43859* (MO); 2 mi. SW of Guatemalan border, Highway 200 to Tapachula, 300 m, *Croat 43771* (MO); Bonampak, near ruins, 500 m, *Matuda 38715* (MO); Mpio. Ocosingo, 5 km SW of Santo Domingo, 600 m, *Davidse et al. 20425* (MO); Esperanza, Escuintla, 150 m, *Matuda 17789* (NY); 6 mi. N of Ocozocoautla, 1000 m, *Croat 40584* (MO); Palenque–Bonampak, 60 mi. SE of Palenque, ca. 400 m, *Croat 40167* (MO); Palenque–Ocosingo, Highway 199, 27 mi. SW of Palenque, 210 m, *Croat 40302* (MO); Cerro Vernal, NW side, 25–30 km SE of Tonalá, 400–600 m, *Breedlove 25617* (DS). **Guerrero**: Tierra Colorada–Xalpatlahuac, Tierra Colorada, Río Comitlán, 900–1000 m, *Croat 45755* (MO); Pinotepa Nacional–Tlaxiaco, Highway 125, ca. 8.4 mi. S of Putla de Guerrero, ca. 1000 m, *Croat 45807* (MO); Tierra Colorada–Acapulco, kms 366–367, ca. 380 m, *Moore & Bunting 8840* (BH). **Jalisco**: Puerto Vallarta, 100 m, *Mexía 1314* (UC); 24.1 mi. from Autlán, ca. 300 m, *Moore & Bunting 8737* (BH); Quimixto, *Mexía 1201* (BM, CAS, DS, G, GH, MO, NY, UC, US). **Nayarit**: Miramar, ca. 10 km W of Jalcocotán, *Dressler & Wirth 2703* (US); Singaita, *Lewis s.n.* (BH); *Philbrick 785* (BH); San Blas, *Lewis s.n.* (BH). **Oaxaca**: Pinotepa–Tlaxiaco, Highway 125, 4.4 km S of Putla de Guerrero, 850 m, *Croat 45835* (MO); 12 km from Hwy. 200, road to Chayuco, 220 m, *Miller & Tenorio L. 524* (MO); Tuxtepec, Rincón del Tigre, Mpio. Acatlán, 2 km from Acatlán on road to Capilla, ca. 100 m, ca. 18°31′N, 96°36′W, *Gereau et al. 2190* (CAS, MO, RSA); Tuxtepec–Oaxaca, 10 mi. S of Valle Nacional, 700 m, *Croat 39802* (MO); 0.5 mi. S of Valle Nacional, 120 m, *Croat 39694* (MO); Esmeralda–Río Verde, Uxpanapa region, 1.1 mi. S of Esmeralda, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63233* (MO). **Puebla**: Teziutlán–Nautla, Rancho Las Margaritas, Hueytamalco, near border with Veracruz, 19°57′N, 97°16′W, *Conradt 218* (MEXU). **San Luis Potosí**: 6 mi. NW of Tamazunchale, 250 m, *Croat 39271* (MO); Tamazunchale, *Lundell & Lundell 7115* (CM); 6.5 mi. S of Matlapa, Ixtiamel, 325 m, 21°18′N, 98°47′W, *Thompson et al. 1320* (CM); *1321* (CM). **Tabasco**: Tacotalpa, *Cowan 1999* (MO). **Veracruz**: 927 m, *Birdsey 226* (UC); Huatusco–Puente Nacional, El Mirador, 21 km E of Huatusco at km 45, ca. 1200 m, *Croat 44014* (MO); near Fortín, Cervecería Moctezuma, 1000–1150 m, *Croat 39408* (MO); Mpio. Nautla, Cuatro Caminos, near Cerro Chico, 30 m, *Ventura 3600* (DS); Mpio. San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, LOTE 71, 400 m, *Ibarra & Colin 3126* (MO), 400 m, 18°34–36′N, 95°04–09′W, *Manríquez & Colin 3126* (MO). NICARAGUA. **Boaco**: along Hwy. 33 from Río Quilan, ca. 300–310 m, 12°35′N, 85°32′W, *Stevens 9335* (MO); Cerro Mombachito, 500–900 m, ca. 12°24–25′N, 85°32–33′W, *Stevens & Grijalva 14749* (MO); Quebrada Río Grande, NE del Cerro Mombachito, 600–700 m, 12°25′N, 85°32′W, *Moreno 354* (MO). **Chinandega**: Río Chiquito, El Viejo, 0–100 m, *Atwood 2635* (MO). **Chontales**: Río Bizcocho–Río El Jordán, 350–550 m, ca. 12°12–16′N, 85°15–17′W, *Stevens & Montiel 22589* (MO); ca. 2.8 km N of Cuapa, 400–500 m, ca. 12°17′N, 85°23′W, *Stevens 3696* (MO); 3 km N of Santo Tomás, 280–300 m, 12°05′N, 85°07′W, *Moreno 16066* (MO); Juigalpa, La Libertad, Río El Bizcocho, ca. 17.4 km NE of Río Mayales, 350–400 m, ca. 12°12′N, 85°17′W, *Stevens 4090* (BM, MO); 4 km NW of Villa Sandino, 100 m, *Davidse et al. 30786* (MO). **Managua**: ca. 4 km from Highway 12, near bridge of Río La Aduana, 80–100 m, ca. 12°02′N, 86°31′W, *Stevens 5394* (BM, LL, MO); Highway 8, ca. 2.4 km SW of intersection with Hwy. 2, km 28, ca. 700 m, 11°57′N, 86°20′W, *Stevens 3990* (MO); 4 km from Highway 8 to Highway 2 intersection, 800–860 m, 11°58′N, 86°18–19′W, *Stevens 4539* (MO); Escuela Nacional de Agricultura and Ganadería, Route 1, 12 km E of Managua, *Atwood 2930* (MO). **Matagalpa**: Matagalpa–Jinotega, km 140, ca. 900–1000 m, *Guzmán et al. 229* (MO); Cerro Musún, ca. 300 m, ca. 12°55′N, 85°16′W, *Stevens 12032* (MO); Quebrada Malacal, Hacienda La Bonanza, ca. 20 km from Matagalpa, 560 m, 13°01′N, 85°47′W, *Castro 2391* (MO). **Nueva Segovia**: 7 km SE de Santa Clara, 600–700 m, 13°40′N, 86°14′W, *Araquistain & Moreno 2191* (HNMN, LE, MO); El Terrero, 4 kms NE of El Jícaro, 500–600 m, 13°45′N, 86°07′W, *Stevens & Moreno 2215* (MO). **Río San Juan**: Río Indio, San Juan del Norte, 2 m, *Araquistain 3312* (K, M, MBM, MEXU, MO). **Rivas**: Volcán Concepción, La Esperanza, 200–400 m, 11°31′N, 85°37′W, *Robleto 1618* (ENCB, MO); Isla Ometepe, 140–350 m, 11°33–34′N, 85°36′W, *Robleto 997* (MO); SE of "La Flor," 300–800 m, 11°32–34′N, 85°37–38′W, *Robleto 1915* (MO); 400–460 m, 11°33′N, 85°37′W, *Sandino 503* (MO). **Zelaya**: road to Mina Nueva America, ca. 10 km from main road, *Stevens 12672* (MO); Ibo Tingni, N of road between Puerto Cabezas and Río Wawa, <10 m, ca. 14°9–11′N, 83°29–31′W, *Stevens 10663* (CM, MO); Puerto Cabezas, 0–20 m, 14°01′N, 83°22–23′W, *Stevens 10684* (MO); Río Blanco–Río Copalar, ca. 29 km E of Río Blanco, 200–400 m, ca. 12°50–55′N, 85°0–05′W, *Stevens 12179* (MO); "Las Mercedes," 160–180 m, *Vincelli 331A* (MO); Matagalpa–Waslala, near Río Las Carpas and Río Babasca, 540–580 m,

13°15′N, 85°32′W, *Sandino 2426* (MEXU, MO); La Luz, ca. 200 m, 13°44′N, 84°47′W, *Ortiz 1606* (F, MO); Cerro Waylawás, E side of Central Range, ca. 100–200 m, 13°38–39′N, 84°48–49′W, *Pipoly 4172* (MO); 6 km SE of Waslala, 520–560 m, 13°16′N, 85°24′W, *Moreno 17279* (MO); Estación Experimental "El Recreo," ca. 15 m, 12°09′N, 84°17′W, *Rios 176* (MO); ca. 80 m, 13°39′N, 84°48′W, *Pipoly 4450* (MO); Río Prinzapolka–Quebrada San Rafael, Waní, ca. 100 m, ca. 13°42′N, 84°50′W, *Pipoly 4593* (MO); ca. 0–100 m, ca. 13°42′N, 84°50′W, *4739* (MO); Río Waní, Boca de Waspuke, 90–100 m, ca. 13°44′N, 84°53′W, *Stevens 7195* (MO); Rama, *Atwood & Moore 897* (MO); Caño Monte Cristo, "La Grupera," ca. 10 m, 11°33′N, 87°48′W, *Moreno & Sandino 14709* (MO); E of campo Germán Pomares, ca. 60–90 m, 11°36′N, 83°52′W, *Moreno 15137B* (MO); ca. 10 m, 11°36′N, 83°51′W, *15187* (MO); Caño Monte Cristo, 1 km before the camp Germán Pomares, ca. 10 m, 12°35′N, 83°51′W, *Moreno 14839* (MO); *14843B* (MO); "Kurinwacito," 80–100 m, 13°08′N, 84°55′W, *Moreno 23699* (F, MO); Cerro El Ocote, 700 m, 13°38′43″N, 85°07′06″W, *Ortiz 1093* (MO); Comarca El Hormiguero, W of Río Uli, *Neill 1921* (MO); Mpio. Rama, Loma Buena Vista, 100–150 m, 12°08′N, 84°12′W, *Robleto 620* (MO); Mpio. Siuna, Siunawás, ca. 200 m, 13°43′N, 84°45″W, *Ortiz 1481* (MO); Santa Rosa, *Ortiz 102* (MO); Negro Wás Sector, El Empalme–Rosita, <200 m, ca. 13°45′N, 84°25′W, *Ortiz 2163* (MO); Río Kubalí, ca. 7 km W of Río Iyas, ca. 200 m, ca. 13°29′N, 85°16′W, *Stevens & Moreno 19278* (MO); Río Matís, Waní–Siuna, ca. 0–100 m, ca. 13°43′N, 84°49′W, *Pipoly 4685* (MO); ca. 0–100 m, *Stevens 4686* (MO. PANAMA. **Bocas del Toro**: S end, Cayo García, 0–5 m, *Peterson & Annable 7287* (MO); Chiriquí Lagoon, *von Wedel 1253* (GH, MO); *2668* (GH, MO); Gualaca–Chiriquí Grande, 4.2 mi. S of Chiriquí Grande, near sea level, 8°55′N, 82°09′W, *Croat 66813* (MO, TEX); Changuinola–Almirante, Station Milla 7.5, <100 m, *Croat 38130* (MO); Río Oeste, S of Almirante, 5 m, *Peterson & Annable 7226* (MO). **Canal Area**: end of Pipeline Road, 19 km NW of Gamboa, 25–50 m, *Nee & J. D. Smith 11070* (MO, US); Fort San Lorenzo, *Maxon & Valentine 7001* (US); 40 m, 9°03′N, 79°37′W, *Croat 69834* (B, CAS, CR, MO); near Madden Dam and along Azote Caballo Road, near Alahuela, 90–100 m, *Dodge 16592* (MO); road to Fort Gulic, *Lazor & Blum 5412* (MO, NY); Barro Colorado Island, *Croat 6586* (MO, NY, US); *Wetmore & Woodworth 874* (GH); *Welch 19833* (MO, NY); *Croat 6066* (MO); *11758* (MO); *9223* (MO); *5878* (MO); *10357* (MO); *12802* (MO); *10744* (MO); *Starry 24* (MO); *Netting 60* (MO); *Hutchison & Wright 2920* (NY, US); *Croat 11744* (MO, SCZ); *10383* (MO, SCZ); *7129* (MO, SCZ); Madden Forest Preserve, vic. George W. Green Park, *Welch 19853* (MO, NY, RSA); Río Pequení, near Salamanca Hydrographic Station, 70–80 m, *Dodge et al. 16592a* (MO); Curundu, 8°58′N, 79°32′55″W, *Croat & Zhu 76204* (MO). **Chiriquí**: W of Gualaca, 100 m, 8°29′N, 82°17′W, *Churchill & de Nevers 4482* (MO, RSA). **Coclé**: El Valle de Antón, *Folsom & Kauke 2776* (MO); *Kennedy et al. 2209* (MO, US). **Colón**: near Palmas Bellas, *Thoms 47* (MO); vic. of Miguel de la Borda, *Croat 9895* (MO); *9885* (MO); 10 mi. SW of Portobelo, 2–4 mi. from coast, 10–200 m, *Liesner 1103* (MO, NY, US); Portobello, 5–100 m, *Pittier 2424* (US); France Field–Cativa1, *Standley 30439* (US); Río Guanche, *D'Arcy 9724* (MO); *Gentry 6313* (MO); 100 m, 9°30′N, 79°39′W, *Croat 75193* (MO). **Darién**: 3 mi. N of Santa Fe, *Tyson et al. 4616* (MO, SCZ); Canglón–Yaviza–Río Chucunaque, 7.7 mi. E of Canglón, 50 m, 8°20′N, 77°50′W, *Knapp & Mallet 3944* (MO, US). **Los Santos**: Tonosí–Jobero, 50–80 m, *Croat 34454* (MO). **Panamá**: Corozal Road, near Panamá, *Standley 26861* (US); *26841* (US); Río Tapia, *28112* (US); 4 mi. E of Panama City, road to Tocumen, *Tyson 3483* (FSU, MO, SCZ); Cerro Jefe region, *D'Arcy et al. 15520* (MO); 9°15′N, 79°30′W, *Croat & Zhu 76215* (CR, MO, P, TEX); San José Island, *Johnston 718* (GH); *919* (GH); *921* (GH, US). **San Blas**: Nusagandi, El Llano–Cartí road, Mile 10.3, 300 m, 9°20′N, 79°W, *Croat & Zhu 76576* (MO). **Veraguas**: S of Santa Fe, ca. 450 m, *Nee 8041* (MO); Bahía Honda, *Elmore H30* (US); ca. 1 km above Cañasas on road to Los Valles, 230 m, *Croat 37063* (MO).

Philodendron hederaceum var. **kirkbridei** Croat, var. nov. TYPE: Costa Rica. Alajuela: eastern rim of Laguna Hule, ca. 1.5 km N of Angeles, along road through pasturelands, 840–860 m, 8 July 1972, *Luteyn 3350* (holotype, MO–2173874; isotype, DUKE). Figure 224.

Planta hemiepiphytica; internodia 2–28 cm longa, 1–2.5 cm diam.; cataphylla 6–19 cm longa, incostata aut interdum leniter 2-costata, decidua intacta; petiolus (6.5)8–22.5 cm longus, 3–6 mm diam.; lamina (11)16–29.5(42) cm longa, (8)10.3–23(35) cm lata; inflorescentia 1; pedunculus 5.5–7.5 cm longus; spatha 14–24 cm longa, lamina spathae flaviviridis, extus cremascenti vs. apicem, intus pallidius viridi; pistilla 5-locularia; loculi 20–25-ovulati; loculi cum ca. 24-seminibus.

Hemiepiphyte; internodes 2–28 cm long, 1–2.5 cm diam., weakly flattened on one side with two sharply raised ribs on the side above petiole, very weakly sulcate on the opposite rounded side, prominently ribbed throughout its circumference, the ribs smooth or prominently warty, 2–28 cm long, 1–2.5 cm diam., medium to dark green, matte, drying reddish brown; cataphylls 6–19 cm long, unribbed or sometimes weakly 2-ribbed, deciduous intact; **petioles** (6.5)8–22.5 cm long, 3–6 mm diam.; **blades** (11)16–29.5(42) cm long, (8)10.3-23(35) cm wide; upper surface medium to dark green, drying brown to greenish brown, lower surface medium green, glossy, drying brown to greenish brown; primary lateral veins 3–4 per side, departing mdirib at a 45–50° angle. INFLORESCENCES 1 per axil; peduncle 5.5–7.5 cm long; **spathe** 14–24 cm long, spathe blades yellow-green becoming cream-colored toward apex outside, lighter green inside; **spadix** stipitate to 1 cm; 13–20 cm long; ovary 5-locular, 20–25 ovules per locule. INFRUCTESCENCE with about 24 seeds per locule.

Flowering in *Philodendron hederaceum* var. *kirkbridei* occurs during the late dry season and early rainy season (probably as early as March and as late as September) based on post-anthesis and early fruiting collections. No collections have been made

at anthesis. Immature fruits have been collected in April, July, and August.

Philodendron hederaceum var. *kirkbridei* ranges from Costa Rica to Ecuador at (250)300 to 900 m in *Premontane wet forest* and *Tropical wet forest.* The variety has been collected only once in both Suriname and Ecuador. It was collected in Ecuador at Reserva ENDESA (0°5′N, 79°02′W), an area of *Premontane rain forest.* It is to be expected in Colombia.

This variety is recognized by its scandent habit, slender stems, petioles shorter than the blades, ovate-cordate brownish-drying blades and especially by its dried stems, which are reddish brown and conspicuously ribbed. Specimens from Panama have stems also conspicuously and densely warty while specimens in Costa Rica have stems reddish brown and conspicuously ribbed but are smooth rather than warty.

The variety differs from the autonymic variety primarily in occurring at generally higher elevations in wetter forests and by its reddish brown, conspicuously ribbed stems. In parts of Central America and in South America where both species occur, *P. hederaceum* var. *kirkbridei* occurs usually above 500 m in *Premontane wet* and *Tropical wet* forests. In contrast, *P. hederaceum* var. *hederaceum* has stems that dry smooth and green and occur primarily in tropical moist forest. Though there is overlap in the elevation range and even life zone (both may sometimes be found in *Premontane wet forest*), the two varieties do not occur in the same sites and can be readily distinguished by their stems.

Philodendron hederaceum var. *kirkbridei* is named in honor of Joseph Kirkbride (BARC), who first collected the taxon in 1968 on Cerro Caracoral in Coclé Province in Panama while a graduate student at the Missouri Botanical Garden.

Additional specimens examined. COSTA RICA. **Alajuela**: Cañas–Upala, 8 km N of Bijagua, 300 m, *Croat 36498* (MO); Cariblanco, 900 m, 10°15′N, 84°11′W, *Lent 3591* (F). **Heredia**: 3 mi. S of Cariblanco, 760 m, *Croat 35837* (MO). PANAMA. **Coclé**: 710–800 m, 8°39′N, 80°36′W, *Croat 68758* (MO, PMA, US); Cerro Caracoral, *Kirkbride 1098* (MO); Alto Calvario, 9.4 km above El Copé, 750–900 m, *Croat 44741* (MO); La Mesa, above El Valle de Antón, 900–930 m, *Croat 37471* (MO); Cerro Gaital, 900–1000 m, 8°37′N, 80°08′W, *Croat 67236* (MO). **Colón**: Río Piedras, Río Piedras Lumber Road, 6.7 mi. E of Sabanitas, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75158* (MO, PMA). **Panamá**: El Llano–Cartí Road, 12 mi. above Pan-American Highway, 200–500 m, *Croat 22909* (MO); Mile 7, near El Llano, 460 m, 9°19′N, 79°59′W, *Croat 75108* (MO, PMA, US); Km 12–16, *Kennedy et al. 3146* (MO, US). **San Blas**: 1 mi. S of Nusagandi, 9 mi. N of Interamerican Highway, 350 m, 9°20′N, 79°W, *Croat & Zhu 77001* (CM, MO).

ECUADOR. **Pichincha**: between Quito and Puerto Quito, Km 113, 800 m, 0°5′N, 79°2′W, *Rodríguez 282* (MO).

Philodendron hederaceum var. **oxycardium** (Schott) Croat, stat. et. comb. nov. Basionym: *Philodendron oxycardium* Schott, Syn. Aroid. *Philodendron scandens* subsp. *oxycardium* (Schott) G. S. Bunting, Gentes Herb. 10: 163. 1968. TYPE: Mexico: exact origin unknown (holotype, W? lost). Schott ic. 2714 (neotype, here designated, W). [See fig. 17 in Bunting, 1968.]

Internodes smooth, sometimes with 2 ridges or weakly angular on one side, semiglossy, 5–26 cm long, to 1 cm diam., usually longer than broad, drying greenish to pale brownish green; cataphylls 19 cm long, unribbed, green; **petioles** 8–23 cm long; **blades** broadly ovate, semiglossy, long-acuminate to abruptly acuminate at apex, cordate at base, 26–32 cm long, 18–22 cm wide (ca. 1.5 times longer than wide), 2.5–3 times longer than petiole, broadest near the middle, upper surface bright green, lower surface yellow-green; sinus narrowly triangular to closed, to 5 cm deep; basal veins 2–3 per side, with 1–2 free to base, and with the first and or second free to base, 2–3 coalesced to 1 cm; primary lateral veins 2–3 per side, departing midrib at a 45° angle. INFLORESCENCES (based on dried specimen) with peduncle 4 cm long, 7 mm diam.; **spathe** 14 cm long; spathe blade 6.5 cm long; spathe tube 7.5 cm long; **spadix** sessile, cylindrical, 12 cm long; pistillate portion 4 cm long; staminate portion 8 cm long; fertile staminate portion drying reddish brown.

Flowering in *Philodendron hederaceum* var. *oxycardium* is poorly known. A single fertile collection with immature fruits in January was seen.

Philodendron hederaceum var. *oxycardium* is apparently endemic to Mexico, known only from the Gulf slope in the states of Jalisco, Nayarit, Oaxaca, San Luis Potosí, and Veracruz at 120 to 580 m, principally in areas of *Tropical moist forest.* Material of *P. hederaceum* [as *P. scandens*] collected in Jamaica (Bunting, 1968) is sterile.

Philodendron hederaceum var. *oxycardium* is similar in appearance to variety *hederaceum*, except that leaves of the former are firmer in texture and glossy in both the juvenile and adult forms. In outline, the leaf blades of *P. hederaceum* var. *oxycardium* are often somewhat broader and more abruptly acuminate than for variety *hederaceum* (Bunting, 1968). The epidermal cells have a more or less

flattened epidermis on the upper surface (Bunting, 1968), which causes it to be glossy. In contrast, the epidermal cells of *P. hederaceum* var. *hederaceum* are mounded and sometimes conical, giving leaves of that variety their characteristic velvety sheen.

Though Bunting (1968) treated this taxon as a subspecies, it appears to overlap geographically with the typical material so it will be treated here as a variety.

Additional specimens examined. MEXICO. **Nayarit**: San Blas, *Ferris 5440* (DS). **Oaxaca**: Tuxtepec–Oaxaca, 6–14 mi. from bridge at Valle Nacional, ca. 580 m, *Moore & Bunting 8905* (BH). **San Luis Potosí**: N of Tamazunchale, *Clark 7408* (MO, NY); Tamazunchale, 120 m, *Aguirre & Reko 334* (NY). **Veracruz**: 5.7–6 mi. from Catemaco on road to Sontecomapan, ca. 380 m, *Moore & Bunting 8937* (BH); just before Papantla on road from Tecolutla, *Moore & Bunting 8953* (BH); NW of Misantla, 2.4 mi. on road to Martínez de la Torre, ca. 320 m, *Moore & Bunting 8944* (BH); Conejo–Huatusco, Km 45, near Puente Nacional, slopes of barranca de Santa María across highway from Hacienda El Mirador, *Moore & Bunting 8869* (BH); Dist. Papantla, *Kelly 16* (BH).

Philodendron heleniae Croat, sp. nov. TYPE: Panama. San Blas: El Llano–Cartí road, 14 km N of Pan-American Hwy., 300 m, 9°15′N, 79°W, 12 July 1988, *Croat 69244* (holotype, MO–3599872; isotypes, B, CAS, COL, CR, F, K, MEXU, NY, PMA, SCZ, US, VEN). Figures 227–230.

Planta plerumque hemiepiphytica, raro terrestris; internodia 4–12 cm longa, 2–3 cm diam.; cataphylla 15–36 cm longa, 1–2-costata, decidua; petiolus teres aut D-formatus, 14–41.5 cm longus, 6–10 mm diam.; lamina anguste ovata, 25–52 cm longa, 6–26 cm lata, in sicco flavibrunnea; inflorescentia 2–10; pedunculus 2–6 cm longus, 4–6 mm diam.; spatha 5–10 cm longa, rubrimarronina; lamina spathae extus pallidiori vs. apicem, intus alba, dilute suffusa marronina; tubo spathae intus atrimarronino; pistilla (5)6–9-locularia; loculi (1)3–4-ovulati.

Usually hemiepiphytic, rarely terrestrial; vining or appressed-climbing, stem appressed-climbing to somewhat scandent, sap tannish; internodes scurfy, 4–12 cm long, 2–3 cm diam., much longer than broad, medium green, drying reddish brown, epidermis smooth or irregularly folded and ridged, sometimes fissured with minute cracks perpendicular to axis, drying with folds longitudinally and usually with fissures transversely; roots dark brown, to 50 cm long, 1–2 mm diam.; cataphylls thin, 15–36 cm long, 1-ribbed to sharply 1-ribbed, or sharply 2-ribbed, green, tinged red, speckled violet-purple, deciduous, rounded, apiculate at apex; **petioles** 14–41.5 cm long, 6–10 mm diam., ± terete or to slightly thicker than broad, or bluntly D-shaped, firm, medium green, tinged violet-purple at base and apex, bluntly flattened adaxially; geniculum 9 mm long, thicker and paler than petiole; **blades** narrowly ovate, subcoriaceous to coriaceous, strongly bicolorous, acuminate at apex (the acumen sometimes apiculate, inrolled, 5 mm long), usually weakly subcordate, sometimes obtuse, truncate or rounded at base, 25–52 cm long, 6–26 cm wide (2–3.37(4.2) times longer than wide), (1.1–1.8(2.30) times longer than petiole), upper surface dark green, semiglossy, drying yellow-brown, lower surface much paler and with dark secretory canals, weakly glossy to matte, drying yellowish to reddish brown; sinus arcuate, 1–1.5 cm deep when present; midrib broadly convex or weakly raised to flat, pale green above, bluntly acute and thicker than broad, reddish slightly paler than surface below; basal veins lacking; primary lateral veins (6–7)8–10(11–13) per side, departing midrib at a 30–40° angle, weakly and narrowly sunken above, raised and paler than surface below; minor veins weakly visible, arising from the midrib only, often interspersed with intermittent secretory ducts, the surface often minutely granular below. INFLORESCENCES 2–10 per axil; peduncle 2–6 cm long, 4–6 mm diam., green, tinged red to reddish; **spathe** recurved (curved downward), semiglossy, 5–10 cm long (1.2–2.5 times longer than peduncle), reddish maroon throughout; spathe blade paler toward apex outside, white, weakly tinged maroon inside; spathe tube 3–4 cm long, dark maroon inside; **spadix** sessile; cylindrical to clavate, protruding forward at anthesis, 5.8–7.5 cm long, ± uniform throughout; pistillate portion pale green to yellowish green, cylindrical to slightly ovoid, 2–3.5 cm long, 5–7 mm diam. throughout; staminate portion cream to white, cylindrical or clavate, 3.4–5 cm long, 6–9 mm diam. at base, 9–10 mm diam. at middle, 5–9 mm diam. ca. 1 cm from apex, broadest at or above the middle, or equally broad throughout, as broad as or slightly broader than the pistillate portion; sterile staminate portion not detectable; pistils 1.4–1.7 mm long, 0.5–1.4 mm diam.; ovary (5)6–9-locular, 0.7 mm long, 0.7 mm diam., locules 0.9–1.2 mm long, 0.3–0.4 mm diam., ovule sac 0.4–1 mm long, with sub-basal placentation; ovules (1)3–4 per locule, 1-seriate, contained within translucent ovule sac, 0.2–0.4 mm long, longer than funicle; funicle 0.1–0.2 mm long (can be pulled free to base), style 0.2–0.4 mm long, 0.4–0.6 mm diam., similar to style type B; stylar canals tiny, difficult to see emerging; style apex flat; stigma discoid or subdiscoid, unlobed, 0.4–0.5 mm diam., 0.1–0.2 mm high, covering entire style apex except for the center; the androecium truncate, margins 4–6-sided, sometimes weakly scalloped; thecae oblong, 0.1–

0.3 mm wide, ± parallel to one another. INFRUCTESCENCE with berries white, 3.3 mm long, 2.4 mm diam.; seeds ca. 6 per berry, reddish brown, 1–1.1 mm long, 0.3–0.5 mm diam.

Flowering in *Philodendron heleniae* occurs in Panama during the late dry season and much of the rainy season, March through October (except April, May, and September). South American collections broaden that range to include the whole year (January through December, except May and September). Post-anthesis collections have been made from June to October.

Philodendron heleniae ranges from Panama (to be expected in the Cordillera de Talamanca in eastern Costa Rica) to Ecuador, from 20 to about 1040(–1450) m elevation in *Tropical wet forest* and *Premontane rain forest* in Panama, Colombia, and Ecuador. In addition, it occurs in pluvial wet forest in Colombia.

Philodendron heleniae is a member of *P.* sect. *Calostigma* subsect. *Oligocarpidium*. This species is characterized by its scandent habit; internodes much longer than broad drying with longitudinal folds and usually transverse fissures; petioles terete to bluntly D-shaped; and narrowly ovate, subcordate, yellow-brown-drying blades with dark secretory canals visible on the lower surface. Especially characteristic are the clusters of 2–10 small inflorescences with externally red spathes.

Philodendron heleniae can be confused with *P. lentii*, which also comprises more or less scandent plants with subcordate leaf blades. That species differs, however, in having one to two large, mostly white inflorescences per axil and more broadly ovate blades drying with many, pale, sunken veins on the upper surface and no dark secretory vessels on the lower surface.

Specimens from the Pacific slope of South America (e.g., *Croat 58424, Tipaz et al. 1318*) are on average larger, with leaves ranging up to 60 cm long and 30 cm wide and with spathes occasionally to 12 cm long. Still, these probably do not differ sufficiently to represent even another subspecies.

Lawrance 817 from Boyacá Department at El Humbo (at 914 m in the Río Magdalena drainage) in Colombia closely matches the material from the Pacific slope. If it proves to be *P. heleniae* it would be the first collection from the Eastern Cordillera of the Andes.

Some South American collections from the Amazon basin may belong to this species. These collections are from both Colombia (*Pipoly et al. 15892, 16027* in Amazonas) and Ecuador (*Gudiño 1160* and *Thomas & Ríos 6708* in Pastaza Province and *Cerón 3360* and *Bennett et al. 4526* in Napo Province). However, most of the collections from the Amazon basin do not mention spathe color, although *Gudiño 1160* indicates the spathes to be greenish red.

Particularly interesting is *Thomas & Ríos 6708*, with spathes described as becoming creamy white, something that never happens with Central American material of *Philodendron heleniae*.

The species was first collected in 1970 by Jim Luteyn and Helen Kennedy in the vicinity of El Valle in Coclé Province, Panama. It is named in honor of one of the collectors, Helen Kennedy, who at the time worked for the Missouri Botanical Garden as the Curator of Summit Herbarium.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, 6.6 mi. N of bridge over Fortuna Lake, 780 m, 8°45′N, 82°18′W, *Croat 66780* (MO). **Coclé**: El Valle region, La Mesa, 800–900 m, 8°38′N, 80°09′W, *Croat 67154* (AAU, CM, KYO, L, MEXU, MO, PMA, TEX, US); El Valle, 5 mi. N of town, 2200 ft., *Hammel & Kress 13427* (DUKE); 8 mi. N of El Valle ca. 880 m, *Luteyn & Kennedy 1734* (DUKE); 880 m, *Croat 37576* (MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76738* (AAU, CM, DUKE, M, MO, S, SEL, TEX); slopes of Cerro Gaital, 800–900 m, 8°37′N, 80°07′W, *McPherson 11209* (L, MO, NY, P). **Darién**: Río Tuquesa, 2 km by air from Continental Divide, vic. of mining camp of Tyler Kittredge, *Croat 27097* (CAS, F, K, MO, PMA, US). **Panamá**: El Llano–Cartí Road, 10.1 mi. above Inter-American Highway, 325–350 m, *Croat 67351* (MO, NY, PMA, US, WIS); Mile 6.8, 350 m, *49106* (MO); Mile 10, 330 m, *33778* (F, MO), *33817* (MO); Mile 7, 460 m, 9°19′N, 79°59′W, *75114* (CAS, MO); 550 m, 9°43′N, 78°60′W, *60502* (MO); Mile 10.6, ca. 400 m, 9°17′N, 78°58′W, *Miller et al. 869* (HUA, MO, PMA); El Valle de Madroño–La Saena, 2.5 mi. N of El Valle de Madroño, 180 m, 9°14′25″N, 79°05′W, *Croat & Zhu 77048A* (MO); Cerro Jefe–Cerro Brewster ["Panama/San Blas"], 600–800 m, 9°17′N, 79°17′W, *Hammel & de Nevers 13553* (MO). **San Blas**: El Llano–Cartí Road, 1–5 mi. N of Nusagandi, 250–300 m, 9°16′N, 79°W, *Thompson 4660* (CM, MO); Nusagandi–Cartí Road, 400 m, 9°18′N, 78°58′W, *McDonagh et al. 93* (BM, MO); ca. 350 m, ca. 9°15′N, 79°W, *McPherson 9762* (MO); 350 m, 78°15′W, 9°19′N, *de Nevers & Todzia 3530* (COL, MO, PMA, QCA, RSA, TEX); 10.1 mi. N of Interamerican Highway, then ca. 0.5 mi. N, Paseo Mariska near road, 300 m, 9°20′N, 79°W, *Croat & Zhu 77020* (MO); El Llano-Cartí Road, 23–29 km from Pan-American Highway, 300–400 m, 9°22′N, 78°69′W, *Knapp 1830* (MO); *1840* (MO, PMA); Km 15, 350 m, 9°20′N, 78°58′W, *Galdames et al. 1288* (PMA); km 17–19, 350 m, 9°19′N, 78°55′W, *de Nevers & Herrera 7963* (CM, MO, US); Cerro Obu, 400–500 m, *de Nevers et al. 8068* (MO, NY). **Veraguas**: Santa Fe region, Alto Piedra–Calovébora, Río Dos Bocas Valley, 350–400 m, *Croat 27370* (F, K, MO, PMA); *27397* (MO).

COLOMBIA. **Antioquia**: Medellín–Bogotá, 12.4 km from entrance to San Luis 800 m, 5°59′N, 74°59′74″W, *Betancur et al. 622* (MO); 4.8 km E of San Rafael, 1040 m, 6°18′N, 75°W, *Brant & Roldán 1486* (HUA); Quebrada Honda, Río Guatapé, *Orozco et al. 898* (COL); Río Guatapé, 1250 m, *Orozco et al. 955* (COL); San Carlos, Finca

"El Desespero," Alto de Samaná, near Miraflores, 4 hrs. SW of Alto de Samaná, 710–820 m, 6°5′N, 74°56′W, *Callejas et al. 8628* (NY); San Luis, Medellín–Bogotá, La Tebaida, 1010–1060 m, 6°8′N, 75°10′W, *Callejas et al. 4015* (MO); Sector Río Samaná–Río Claro, 750 m, *Hernández et al. 551A* (HUA); San Luis–Puerto Triunfo, SE of Granada, S of San Carlos, ca. 3 km SE of San Luis, ca. 800 m, 5°57′N, 74°57′W, *Croat 52038* (COL, MO, NY); Gómez Plata–Yolombo border, Sector La Cancana, along Río Porce, km 14 via Amalfi, 1030 m, *Callejas et al. 2338* (MO); Sonson, Rioverde region, Hacienda "La Soledad," on the banks of Quebrada "Curubital," *Gutiérrez 35552* (UC); Amalfi–Fraguas, NE of Salazar, 23–26.5 km from center of Amalfi, 1220–1300 m, 6°58′N, 74°59′W, *MacDougal et al. 4042* (MO). **Chocó**: Bahía Solano, S of airport, ca. 100 m, 5°13′30″N, 76°21′30″W, *Croat 57458* (CHOCO, COL, JAUM, MO, US); ca. 2 km E of Playa de Oro, ca. 200 m, 5°20′N, 76°23′W, *Croat 57424* (CHOCO, COL, MO); Mecana (N of Bahía Solano), Quebrada Resaquita, 30 m, *Juncosa 2536* (MO); Quibdó–Istmina, 6.6 km S of Quibdó, <100 m, 5°33′N, 76°37′W, *Croat & Cogollo 52156* (MO); Río Pató, Las Animas–Pató, Serranía de Baudó, 10 km SE of Pató, 5°17′N, 76°45′W, *Croat 56071* (MO), *Croat 56107* (MO); Río Sucio, Cerro del Cuchillo, zona de Urabá, 520 m, *Cárdenas 468* (MO); Parque Nacional de Utría, Río San Pichí, 0–100 m, 6°20′N, 77°20′W, *García & Agualimpia 458* (MO); Río San Juan, Quebrada del Taparal, 5–20 m, *Cuatrecasas 21462* (F). **Risaralda**: Mpio. Mistrato, corregimiento San Antonio de Chamí, vereda la Unión, carretera hacia La Mesenia, 1450–1700 m, 5°28′N, 75°54′W, *Betancur et al. 3520* (MO). **Valle**: Cali–Buenaventura, Río Digua valley, 1 km E of La Cascada, 340 m, *Croat 38579* (MO, PMA); Bajo Calima area, Quebrada La Sierpe, 5 m, 4°10′N, 77°10′W, *Forero et al. 4006* (MO); Bahía Málaga, 0–20 m, 4°N, 77°30′W, *Gentry et al. 53362* (MO); carretera Gasolina 6 km S of main road between Calí–Buenaventura highway and Málaga, 50–80 m, 3°56′N, 77°07′30″W, *Croat 69411* (CM, MO); 22.3 km beyond Pulpapel Headquarters, 4°02′N, 77°07′W, *Croat 61275* (CUVC, MO). ECUADOR. **Carchi**: Tulcán, Reserva Indígena Awá, 650–100 m, 1°N, 78°24′W, *Tipaz et al. 1318* (MO, QCNE). **Esmeraldas**: Lita, 550–650 m, *Madison et al. 4990* (F, K, SEL); Lita–San Lorenzo, Km 18, 0°55N, 78°28W, *Croat 72389* (MO); San Lorenzo, Mun. Ricaurte, Reserva Indígena Awá, 300 m, 1°10′N, 78°32″W, *Tipaz et al. 2068* (MO); Río Jordán, NE of Las Golondrinas, near San Isidro, 300 m, 0°20′N, 79°12′W, *Palacios 11485* (MO, QCNE). **Imbabura**: Lita, 600 m, *Cobb 29* (MO). **Pichincha**: Río Verde, 2 km SE of Santo Domingo de Los Colorados in Cooperative Santa Marta #2, 530 m, *Dodson 7403* (MO, QCNE); Santo Domingo de los Colorados, Río Baba, 28 km S, 350 m, *Dodson & Thien 1187* (MO).

Philodendron immixtum Croat, sp. nov. TYPE: Panama. Panamá: Comarca de San Blas, Río Playón Chico, 50–100 m, *H. Herrera et al. 1167* (holotype, MO–4256423; isotypes, AAU, K, MEXU, PMA, US). Figures 233–236.

Planta hemiephytica; internodia (2)10–15 cm longa, (7 mm) 1–1.5 cm diam.; petiolus subteres, actue D-formatus ad debiliter planatus; lamina anguste ovata vel ovato–elliptica, 16–36 cm longa, 5–12 cm lata; inflorescentia solitaria; pedunculus 5–13 cm longus; spatha 9–19 cm longa, lamina albo-viridis vel alba, tubo viridis extus, rubo vel purpureo intus; spadix 10–11 cm longus; ovarium (3)4–6(8)-loculare; loculi 1(2) ovulati.

Hemiepiphytic; stem scandent, sap reddish, watery; internodes long, slender, ± glaucous, (2)10–15 cm long, (0.7)1–1.5 cm diam., much longer than broad, dark olive-green matte to weakly glossy, becoming gray-green, drying light brown, epidermis sometimes cracking with loose flakes; roots ca. 5 per node, to 15 cm long, 2–3 mm diam., tannish gray, drying reddish brown, ± smooth, long; cataphylls somewhat spongy, to 17 cm long, unribbed, weakly 2-ribbed or sharply (1–)2-ribbed (ribs 2 mm high), pale green, dark short-lineate, drying pale brown to yellowish brown, usually some deciduous, sometimes persisting somewhat intact, eventually fibrous, obtuse at apex, margins paler, yellowish; **petioles** 7.5–16(21) cm long, 2–10 mm diam., subterete, sharply D-shaped to slightly flattened adaxially, rounded abaxially, surface dark green-striate, matte to semiglossy, shortly dark lineate, with dark green ring around apex; **blades** narrowly ovate to ovate-elliptic, or rarely oblong-elliptic, subcoriaceous, semiglossy, strongly bicolorous, abruptly acuminate at apex (the acumen tightly inrolled to apiculate, 2–4 mm long), subcordate, rarely rounded at base, 16–36 cm long, 5–12 cm wide (1.9–3.7 times longer than wide), (1.3–3.1(3.8) times longer than petiole), about twice as long as petiole, broadest below middle, margins narrowly hyaline, upper surface drying green to grayish to brownish green; posterior lobes short, about as broad as long and held close to petiole; sinus shallow, 0–2.5(3) cm deep; midrib flat to weakly convex, concolorous or slightly paler than surface above, convex to bluntly acute, paler than surface below; basal veins lacking; primary lateral veins 4–8 per side, departing midrib at a 50–60° angle, ± straight to weakly arcuate to the margins, sunken and paler than surface above, weakly raised and darker than surface below; interprimary veins weakly raised and darker than surface; minor veins distinct to weakly visible, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 5–13 cm long, 3–7(11) mm diam., dark green; **spathe** 9–19 cm long, (1.1–2.1 times longer than peduncle), green, densely and obscurely short-lineate, narrowly acuminate at apex; spathe blade pale greenish white to white outside, pale greenish white, dark lineate inside; resin canals appearing as continuous lines, drying reddish brown, resin droplets forming on spathe surface within; spathe tube dark green in back, paler in front on open edges outside, red or violet-purple inside; **spadix** gradually tapered to apex,

protruding out of the end of spathe, bluntly rounded to obtuse at apex, 10–11 cm long, broadest above the middle, constricted slightly above sterile staminate portion; pistillate portion pale green, cylindrical, 3.4–4.2 cm long, 3.7 cm long in front, 2.7 cm long in back, 9–11 mm diam. at apex, 10–11 mm diam. at middle, 9–11 mm wide at base; staminate portion 6.8–7.5 cm long; fertile staminate portion white, cylindrical to clavate, 9–12 mm diam. at base, 1.1–1.3 cm diam. at middle, 7–12 mm diam. ca. 1 cm from apex, broadest at the middle, broader than the pistillate portion, broader than the sterile portion; sterile staminate portion as broad as, narrower than, or broader than the pistillate portion, ± 12 mm diam.; pistils 1.9–2.3 mm long, 1.3–1.9 mm diam.; ovary (3)4–6(8)-locular, walls sometimes embedded with granular, crystal-like particles, locules 0.7–1.3 mm long, 0.4–0.7 mm diam., ovule sac 0.6–1.3 mm long, with subbasal placentation; ovules 1(2) per locule, contained within transparent ovule sac, 0.4–0.7 mm long, longer than funicle; funicle 0.2–0.6 mm long (can be pulled free to base), style 0.3 mm long, 0.9–1.4 mm diam., similar to style type B; stigma subdiscoid, unlobed, 0.7–0.9 mm diam., 0.2 mm high; the androecium truncate, margins 4–6-sided; thecae oblong to slightly elliptical, 0.4 mm wide, ± parallel to one another; sterile staminate flowers 4–6-sided, 1–1.8 mm long, 1.1–1.7 mm wide. INFRUCTESCENCE with spadix yellowish orange, 8 cm long, 3 cm wide; berries concave at apex; seeds 1 per locule, 1.5–1.8 mm long, 0.6–0.7 mm diam., yellow-brown.

Flowering in *Philodendron immixtum* occurs during the last half of the dry season and the first part of the rainy season, March through May, with post-anthesis inflorescences seen from March through August, and fruits seen in July.

Philodendron immixtum ranges from Panama to Colombia (Golfo de Urabá), occurring at or near sea level (to ca. 140 m elevation), primarily along the Atlantic slope in Colón and Panamá Provinces but also in Panamá Province on the Pacific slope along the Río Majé. It occurs in *Tropical wet forest, Premontane wet forest,* and in wetter parts of *Tropical moist forest* life zones.

Philodendron immixtum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* The species is characterized by its scandent habit; long, slender, mostly light-brown-drying internodes; slightly flattened petioles (about one-half or less as long as the blade); narrowly ovate to ovate-elliptic, green-drying blades, which are usually cordulate at the base; as well as by the solitary inflorescence with a green spathe, the base white on the blade at anthesis and red within on the tube.

The species has been confused with *P. inconcinnum* Schott (1856) (hence the name "immixtum," meaning "intermixed or mingled with") from Venezuela (Standley, 1944; Croat, 1978). The Schott paintings of *P. inconcinnum* show a single unattached leaf and unattached inflorescences and probably represent the same species as *P. sphalerum* Schott (1860). Schott paintings of *P. sphalerum* show some leaves that are virtually identical to the above-mentioned drawings. *Philodendron sphalerum* differs from *P. immixtum* in having several small inflorescences per axil (rather than one, somewhat larger inflorescence for *P. inconcinnum*). Schott's original description of *P. sphalerum* did not mention an inflorescence, so his drawing of that must have come later than his description. Schott's original description of *P. inconcinnum* cited Venezuela as the type locality, not Panama, and the solid greenish inner spathe surface depicted in his paintings corresponds well to *P. sphalerum* but not to the material in Panama, which has a reddish interior spathe surface.

Philodendron immixtum has also been confused with *P. ligulatum.* The latter species differs in having blades that are typically more nearly oblong-elliptic to narrowly obovate-elliptic, frequently broadest above the middle, and drying usually much blackened. In addition, it has petioles that bear a conspicuous purple ring around the petiole at the apex. In contrast, the blades of *P. immixtum* typically dry grayish to brownish green and are broadest frequently below the middle. The species also differs in having petioles that lack the purple ring at the apex.

A number of sterile or immature collections from Nicaragua may represent this species, but if so it is curious that the species has not been collected in Costa Rica (or for that matter, not further west in Panama than Miguel de La Borda in Colón Province).

Additional specimens examined. PANAMA. **Canal Area**: Balboa, *Standley 28542* (US); Ft. Randolph, *28616* (US); road between Gatún Locks and Ft. Sherman, ca. 1 mi. E of Ft. Sherman, <25 m, 9°19′N, 79°57′30″W, *Croat & Zhu 76282* (CR, GB, MO, PMA, TEX, US); Ft. Sherman, from Pina to 3 mi. NE, *Liesner 1382* (MO, US); Barro Colorado Island, *Croat 5064* (MO), *10865* (MO, SCZ); *Shattuck 851* (F, MO); *Wetmore & Woodworth 11* (F, GH); *Aviles 89* (F); *Fairchild 3079* (US); Parque Nacional Soberania, 140 m, 9°06′20″N, 79°37′20″W, *Croat & Zhu 76987* (MO). **Colón**: 0.25 mi. N of María Chiquita on road to Portobelo, *11360* (F, MO); Río Indio–Miguel de la Borda, along ocean trail, 0 m, *36898* (MO); vic. of San Miguel de la Borda, *9896* (MICH, MO, NY, PMA, SCZ); 2 mi. W of Portobelo, *33574* (BR, DUKE, MO); Palma Bellas–Sal-

ud, near sea level, *36865* (MO); 4.5 km SW of Piña, 0–5 m, *Nee 11713* (MO); 3 km S of Piña, 50 m, *Sullivan 137* (MO); Portobelo, *Croat & Porter 15613* (MO); Nuevo Tonosí–Río Indio, near sea level, *Croat 33545* (MO). **Darién**: Cerro Pirre, 17 km N of El Real, along Río Perisenico, 100 m, 8°01′N, 77°44′W, *Croat & Zhu 77093* (CM, MO); *77162* (CM, MEXU, MO, PMA, US). **Panamá**: Río Maje, W of Bayano Lake, ca. 2 mi. upstream, 30–60 m, *Croat 34592* (MO).

COLOMBIA. **Chocó**. Mpio. Acandí, Golfo de Urabá, Bahía Zardí, 0–5 m, 8°23′N, 77°07′W, *Betancur et al. 1238* (HUA, MO).

Philodendron jacquinii Schott, Syn. Aroid. 90. 1856. TYPE: Plate 152 in Jacq., Select Stirp. Amer. Hist. 1763 (holotype). Figures 231–232, 237, 241–242.

Philodendron hoffmannii Schott, Oesterr. Bot. Z. 8: 178. 1858 (as "*P. hoffmanii*"). TYPE: Costa Rica. *Hoffmann s.n.* (holotype, B destroyed). Schott ic. 2507 (neotype, here designated, W).

Philodendron deviatum Schott, Bonplandia 7: 29. 1859. TYPE: Venezuela, *Fendler 1329* (lectotype, here designated, K).

Philodendron erlansonii I. M. Johnston, Sargentia 8: 89, t. 13. 1949. TYPE: Panama. Panamá: Perlas Archipelago, San José Island, along road about one-half mi. E of Red Hill, 31 Dec. 1945, *Johnston 967* (holotype, GH).

Philodendron apocarpum Matuda, Madroño 10: 171. 1950. TYPE: Mexico. Chiapas: along Río Cintalapa, at Gilguero, 15 km E of Escuintla, Chiapas, ca. 200 m, 10 Aug. 1948, *Matuda 18313* (holotype, MEXU; isotypes, F, MEXU).

Hemiepiphytic vine; stem scandent, green to gray-brown, glossy, setose-pubescent; leaf scars conspicuous, 1 cm long, 1 cm wide; internodes elongate, 6–25 cm long, 0.8–1.5 cm diam., longer than broad, brownish gray, semiglossy, weakly asperous, epidermis paper-thin, sometimes peeling with age, drying gray-green to yellowish green, matte, sometimes almost blackened, larger stems drying yellow-brown and finely ridged; roots few per node, short, ca. 1 mm diam., light brown, sparsely scaly; cataphylls unribbed, semiglossy, 6–10 cm long, light green, translucent, drying cream-colored, deciduous intact; **petioles** 7.5–44.5 cm long, 5–10 mm diam., subterete, medium green, weakly glossy, narrowly and obtusely sulcate adaxially, surface setose-pubescent, often puberulous; **blades** broadly ovate-cordate, thin, chartaceous, acute to shortly acuminate, sometimes mucronate at apex (the acumen sometimes apiculate, 1–3 mm long), cordate at base, (10.5)11.5–39 cm long, 7.5–28 cm wide (0.99–1.8 times longer than wide), (0.6–1.85 times longer than petiole), usually about equal in length to petiole, broadest near point of petiole attachment, upper surface dark green, matte to subvelvety to weakly glossy, lower surface moderately paler, weakly glossy to almost matte, moderately paler; anterior lobe 8.3–27 cm long, 9–28 cm wide (1.6–3.4 times longer than posterior lobes); posterior lobes ± rounded, 3–13.5 cm long, 3.4–13.6 cm wide, directed inward at maturity, rounded or obtuse; sinus ± narrowly parabolic; midrib broadly convex, concolorous above, broadly convex to round-raised, often setose-pubescent near base, slightly paler below; basal veins 3–6 per side, with 0–1 free to base, 1–2 coalesced 0.5–2.5 cm; posterior rib not naked or briefly naked for 0.5 cm (rarely to 1.5 cm); primary lateral veins 2–3(4–5) per side, departing midrib at a 45–55° angle, ± straight to the margins, prominently impressed to weakly convex above, convex to round-raised below; minor veins arising from both the midrib and primary lateral veins; tertiary veins obscurely visible to raised and conspicuous, darker than surface below. INFLORESCENCES erect, 1 per axil; peduncle (2)4–15 cm long, (2)3–6(7–13) mm diam., green, dark-striate, glabrous; **spathe** 10–16.5 cm long, (0.96–2.3(2.7–3) times longer than peduncle); spathe blade green outside, red inside; spathe tube inflated bulbous, green outside, 4 cm long, white or green inside; **spadix** sessile; 8–13 cm long, narrowly rounded at apex; pistillate portion 3–3.5 cm long, 3.5 cm long in front, 3 cm long in back, 3.5 cm diam. throughout; staminate portion 9.2 cm long; fertile staminate portion 1.5–1.6 cm diam. at base, 1.1 cm diam. at middle, 1 cm diam. ca. 1 cm from apex; sterile staminate portion narrower than the pistillate portion, 1.2–1.5 cm diam.; pistils 6.5–7.2 mm long, 2 mm diam.; ovary 4-locular, locules ca. 1.3 mm long, ca. 0.6 mm diam., with sub-basal placentation; ovules 2 per locule, contained within transparent, gelatinous matrix (no true envelope), 0.6–1 mm long, as long as or longer than funicle; funicle 0.4 mm long (can be pulled free to base), style similar to style type B; style apex quite rounded; styles usually elongated to 5 mm long, sometimes essentially sessile; stigma hemispheroid to sometimes somewhat globular, lobed, 3.3 mm diam., 1.5 mm high, covering entire style apex; the androecium truncate, prismatic, some oblong, margins irregularly 4–6-sided, 1–1.7 mm long; thecae oblong, 0.5 mm wide, ± contiguous; sterile staminate flowers irregularly 4–5-sided, 2.2 mm wide. INFRUCTESCENCE usually pendent, often from leafless stems; peduncle 7–15 cm long, recurved; spathe falling free; spadix (2.5)5–9(14) cm long, (1.5)2.5–7 cm wide; berries greenish when immature, pale orange to red to reddish orange when mature, irregular, 1 cm long, 5 mm diam.; seeds 4–6 per berry, white, ovoid, 4 mm long, 3–4 mm diam., moderately sticky. JUVENILE

plants with petiole margins vaginate-winged almost to one-half their length; blades narrowly ovate-cordate.

Flowering in *Philodendron jacquinii* occurs in August but most post-anthesis collections are from the rainy season, mostly June through September (but also November, January, and March). Immature fruits are known from virtually throughout the year, and mature fruits from March, June, and July. There seems to be little phenological variation in this species.

Philodendron jacquinii ranges from Mexico to Panama on both slopes of the Continental Divide to northern Colombia, Venezuela, and the Guianas, as well as western Cuba and the Cayman Islands, from sea level to 1500(2500)m elevation (mostly below 300 m), mostly in *Tropical moist forest* but also in *Tropical dry forest, Premontane moist forest,* and *Premontane wet forest* life zones.

This species, the only member of *P.* sect. *Macrogynium,* is distinguished by occurring in moderately low, dry habitats, and by its scandent habit, elongate internodes, setose-pubescent stems, petioles and veins of lower blade surfaces, subterete petioles (about equal the blades in length), and thin, ovate-cordate veiny blades. Especially characteristic are the generally swollen spathe tubes and elongated styles, making the pistillate portion of the spadix much broader than the staminate portion.

Philodendron jacquinii may be confused with *P. brevispathum,* another species with scaly petioles and thin blades with prominent posterior lobes. The latter species differs in having ovate-triangular blades with more slender, frequently flaring posterior lobes and a reddish brown stem with simple or branched scales lacking the elongated setae typical of *P. jacquinii,* which has typically greenish stems. In addition, the berries of *P. jacquinii* are pale orange to reddish, and the spathe is reddish within (vs. berries whitish and the spathe green within for *P. brevispathum*).

For a discussion of the long-standing nomenclatural confusion involving *P. hederaceum,* see under the latter name. Although Standley and Steyermark (1958b), in their treatment of Araceae for the *Flora of Guatemala,* had the taxonomy correct in regards to this confusion, their illustration labeled *P. hederaceum* (fig. 58) appears to be a mixture of the two species, with the leaves of *P. hederaceum* and an inflorescence of *P. jacquinii.* The former species differs in lacking the setose-pubescence and scales characteristic of *P. jacquinii,* and in having more coriaceous blades as well as normal, short, closely compacted pistils. The spathe tube of the latter is also not markedly inflated.

A collection from El Salvador (*Croat 42075*) is unusual in lacking the usual trichomes on the stems.

Philodendron lundellii Bartlett ex Lundell (Bartlett, 1937) also corresponds to this species, but the name was invalidly published (without a description or Latin diagnosis).

Additional specimens examined. BELIZE. **Belize**: Western Highway, Mile 35, *Croat 24784* (F, MO); Belmopan, *Gentry 8423* (MO); 9.5 mi. S of Georgeville, road to Augustine, *Croat 23479* (MO); Hummingbird Highway, 7 mi. S of junction with Western Highway, N boundary of Roaring River Est., ca. 110 m, *Spellman & Newey 1967* (GH, MO). **Corozal**: *Gentle 530* (CM, MICH); Cerro Maya Ruins, Lowry's Bight, *Crane 510* (LL), *418* (LL, MO); *Gentle 345* (MICH). **Orange Walk**: Honey Camp, *Lundell 99* (F, US); 2 mi. N of Orange Walk, *Sutton et al. 122* (BM). **Toledo**: Maya Mountains, lower slopes of Richardson Peak, N of junction of Richardson Creek and Bladen Branch, 300–620 m, 88°46′30″W, 16°33–35′N, *Davidse & Brant 31955* (B, MO). COSTA RICA. **Alajuela**. Orotina, Valle del Tárcoles, 100 m, *Hammel & Grayum 19932* (CR, INB). **Guanacaste**: El Mirador, 450 m, *Aguilar et al. 1343* (INB, MO). **Heredia**: La Selva Field Station, ca. 100 m, *Hammel 10500* (MO); 1.4 km NW of Puerto Viejo, 75 m, *Anderson & Mori 25* (CM). **Puntarenas**: Barranca Site, 15 mi. N of Puntarenas, *Janzen 10742* (MO); Los Barrancas, along Pan-American Highway, near Miramar turnoff, *Gentry 774* (MO); Río Guacimal, San Luis, Monteverde, 700 m, 10°16′N, 84°49′W, *Bello et al. 20* (CR, MO); Monteverde Reserve, 1500 m, ca. 10°17′N, 84°48′W, *Croat 61192* (CM, MO); 1300 m, *Haber & Bello 7983* (CR, MO); Cantón de Buenos Aires, along Río Ceibo, Ujarrás, 500 m, 9°14′N, 83°18′W, *Grayum 10228* (CR, INB, MO, US). **San José**: Mora, Colón–Hacienda El Rodeo, 800 m, 9°55′N, 84°16′W, *Hammel 18579* (INB, MO). EL SALVADOR. **Ahuachápan**: San Francisco Menéndez–Tacuba, 0–2 mi. NE of San Francisco Menéndez, 200–450 m, *Croat 42075* (MEXU, MO). GUATEMALA. **Without locality**: *Heyde 463* (US); *Aguilar 309* (F). **Chiquimula**: Río Chiquimula, Santa Bárbara–Petapilla, 4–6 mi. N of Chiquimula, 350–420 m, *Standley 30245* (F); Las Mamacas, 16 mi. S of Guatemala City on CA-9, 3800 ft., *Dziekanowski et al. 3472* (UMO). **Jalapa**: Jalapa–San Pedro Pinula, 1400–1800 m, *Standley 77051* (F). **Jutiapa**: *Standley 75385* (F); *75695* (F); *75212* (F); El Barrial, E of Jutiapan, ca. 800 m, *Standley 75764* (F); Jutiapa–Las Tunas, NW of Jutiapa, 850–900 m, *Standley 76294* (F). **Petén**: 31 km S of Flores, 175 m, *Harmon & Dwyer 2797* (MO); La Libertad, *Lundell 2551* (MICH); 1 km S on old trail to Mahaquila, *Contreras 2912* (LL); Tikal National Park, *Lundell 15292* (LL); *16792* (LL); *Contreras 343* (LL); Dolores, *Contreras 3763* (LL). **Retalhuleu**: Nueva Linda–Chaperico, 120 m, *Standley 87774* (F). **Santa Rosa**: SE of Barberena, 1100–1800 m, *Standley 77740* (F); Cuilapilla, 900 m, *Standley 78087* (F); La Sepultura region, W of Chiquimulilla, 220 m, *Standley 79331* (F); Chiapas, 3500 pp, *Heyde & Lux 3867* (US); Yaxoquintela, floodplain of Río Santa Cruz (upper tributary of Río Usumacinta), 560 m, 16°58′N, 91°47′W, *Rawlins 93* (CM). **Zacapa**: trail between Río Hondo and waterfall, 250–400 m, *Standley 29396* (F); Quebrada

Alejandria, summit of Sierra de Las Minas, Finca Alejandria, 2500 m, *Steyermark 30856* (F); Mpio. Ocozocoautla, E edge of Selva del Ocote, 900 m, *Breedlove 70760* (CAS, MO). HONDURAS. **Colón**: Trujillo, Capuchin Monkey Site West, *Saunders 523* (MO); Bonito Oriental–Limón road, ca. 50 m SW of Río Piedra Blanca, 40 m, 15°46′30″N, 85°41′W, *Evans 1086* (MO). **Copán**: 10 mi. W of Copán, road to La Entrada, 700 m, *Croat 42517* (MO). **Morazán**: Río Yeguare drainage, ca. 14°N, 87°W, *Williams 15908* (F); Río Yeguare, E of El Zamarano, ca. 750 m, *Standley 15448* (F); Río de la Orilla region, SE of El Zamorano, 900–950 m, *Standley 22404* (F). **Olancho**: Juticalpa, 380–480 m, *Standley 17524* (F); Río Olancho, Gualaco–San Bonito Oriental, 7.4 mi. NE of San Esteban, 540 m, 15°20′N, 85°42′W, *Croat & Hannon 64363* (MO). **Yoro**: Río Aguán, Coyoles, *Yuncker et al. 8663* (F, GH, MICH, MO, NY, US); Río Guaymón, La Cieba–San Pedro Sula, SW of Tela, near border of Yoro and Atlántida, 50 m, 15°30′N, 87°43′W, *Croat & Hannon 64666* (MO). MEXICO. *Hahn s.n.* (P). **Campeche**: Yucatán Peninsula, Champoton, *Steere 1742* (CM); Maskall, *Gentle 1186* (CM, MICH, NY); Tuxpena, *Lundell 1074* (F). **Chiapas**: Arriaga–Las Cruces, 5.7 mi., ca. 160 m, *Moore & Bunting 8923* (HB); 51 mi. NE of Chiapas–Oaxaca border on Hwy. 190 to Tuxtla Gutiérrez, 660 m, 16°47′N, 93°18′W, *Thompson et al. 432* (CM, MO); 5 mi. N of Ocozocoautla, along road to Apitpac, 1000 m, *Croat 40544* (MO); Río Cintalapa, Aguas Calientes, Escuintla, *Matuda 18312* (NY); Esperanza, Escuintla, *Matuda 18314* (MEXU, MO); Mpio. Berriozábal, 5 km E of Berriozábal, along Mexican Hwy. 190, 800 m, *Breedlove & Thorne 30412* (MO); Mpio. Ocosingo, Río Usumacinta, 3 km. S of Frontera Corozal, 120 m, *Martínez S. 7309* (MO); Mpio. Ocozocoautla, km 103–104 Hwy. 190, 15.7 mi. E of Cintalapa, 3050 ft., *Bauml & Kimnach 527* (US); Río Grijalva, 10 km S of Hwy. 190 on road to Acala, at Nandaburri, 1600 ft., *Laughlin 2811* (F). **Guerrero**: Acapulco, *Palmer 462* (US). **Oaxaca**: Tuxtepec–Matias Romero, <100 m, *Croat 78724* (CHIP, MO); 7.5 mi. SW of Tuxtepec on road to Valle Nacional, *Moore & Bunting 8908* (HB); 14 mi. N of Puerto Escondido on Rte. 131 to Oaxaca, 300 m, 16°13–47′N, 97°5–8′W, *Thompson et al. 424* (CM, MO); 5 mi. N of Palmar, 54 mi. N of junction of Highways 185 and 190, along Hwy. 185, 65 m, *Croat 40002* (MO); Parque Nacional de Laguna Temazcal, Temazcal, 150 m, 18°25′N, 96°25′W, *Hammel & Merello 15454* (MO). **Quintana Roo**: Mpio. Chetumal, 6.5–7 km N of Tomás Garrido on the road joining Hwy. 186 W of Nicolas Bravo, 150 m, 18°6′N, 89°3′W, *Saunders et al. 9950* (MO); 1 km E of Chanca Veracruz, *E. Cabrera & H. Cabrera 4981* (MEXU). **San Luis Potosí**: Tamazunchale, *Edwards 549* (F, MO). **Veracruz**: Córdoba–Veracruz, Ejido San José de Gracia below Penuela, *Moore & Bunting 8877* (HB); San Lorenzo Tenochtitlán, 22–75 m, *Wing 50* (GH). **Yucatán**: *Schott 489* (BM); Mérida, *Gaumer 489* (BM, F); Izamal, *Gaumer 23174* (F) *Gaumer 1422* (F); *Greenman 376* (F); *Gaumer 23823* (F, US). NICARAGUA. **Boaco**: Las Pitas, Camoapa, 400 m, 12°28′N, 85°35′W, *Moreno 10643* (MO); Río Las Cañas, along Hwy. 33, ca. 3.1 km N of Hwy. 35 intersection, ca. 275 m, 12°38′N, 85°33′W, *Stevens 5838* (MO). **Chontales**: Route 7, 5 km SE of Juigalpa, *Moore 1622* (MO). **Granada**: Laguna de Apoyo, 110–180 m, 11°53′N, 86°01′W, *Moreno 11178* (MO). **Masaya**: Parque Nacional Volcán Masaya, N slope of Volcán Santiago, ca. 375 m, 11°59′N, 86°10′W, *Stevens 5267* (BM, MO); summit of Volcán Masaya, 500 m, *Stevens 2950* (MO); Piedra Quemada, 2 km E of Volcán Masaya, 250 m, *Stevens 4606* (BM, MO). **Matagalpa**: Ranchería, 11 km NE de Muy Muy, ca. 280 m, 12°46′N, 85°31′W, *Moreno 24483* (AAU, MO); Río Yasica, Tuma, ca. 28 km NE Matagalpa, El Diamante, ca. 350–400 m, 13°04′N, 85°46′W, *Guzmán et al. 915* (MO). **Río San Juan**: Boca de Sábalos, "La Toboba," 70–90 m, 11°03–04′N, 84°28–29′W, *Robleto 1833* (US). **Rivas**: Tola–Las Salinas, El Coyol, ca. 2.3 km beyond entrance of Hda. Miramar, ca. 30–40 m, 11°23′N, 85°58′W, *Stevens 9749* (BM, MO). **Rivas–Carazo–Granada**: Río La Pita–Río Escalante, ca. 20 m, 12°34′N, 86°08′W, *Stevens 9718* (BM, MO). **Zelaya**: SW of Puerto Cabezas, 0–2 m, 14°01′N, 83°24′W, *Stevens 7880* (MO); Mpio. Siuna, Wany, *Ortiz 59* (MO). PANAMA. **Canal Area**: Balboa, *Standley 29256* (US); road S-10 N of Escobal, *Croat 12458* (MO, NY, U); Rodman Marine Base, Rodman Naval Ammunition Supply Depot, W of Balboa, 70–80 m, 8°58′N, 79°36′25″W, *Howard 147* (MO); road to Cerro Pelado Radar Station, 0.5 km NW of Gamboa, 75–150 m, *Nee 7760* (MO, RSA); Curundu, Parque Metropolitano, 8°58′N, 79°32′55″W, *Croat & Zhu 76202* (MO); Gamboa, *Croat 74755* (F, MO); Geologic Test Site N of Paraíso, *Croat 12977* (MO); near Summit Hills Golf Course, *Croat 10956* (MO); Gaillard Hwy., vic. Summit Golf Club, 40 m, 9°03′N, 79°37′W, *Croat 69835* (AAU, MO, US); Radar Station Road, 1 mi. N of Summit Gardens, *Croat 9080* (MO); Barro Colorado Island, *Shattuck 115* (F, GH); *Zetek 4675* (MO, US); Wheeler 5, *Shattuck 215* (MO); laboratory clearing, *Croat 10261* (MO); *9259* (MO); Colorado Point, *Croat 6138* (MO); Vista Alegre, *Zetek 5576* (MO); Chagres River, vic. of Juan Mina, Flat Rock, *Bartlett & Lasser 16839* (MICH, MO); Fort Clayton, vic. of end of C-16 road, *Blum 2243* (MO, SCZ); Ft. Sherman, *Standley 31020* (US); Madden Dam Area, Boy Scout Road, *Porter et al. 4062* (MO); Madden Forest, Las Cruces Trail, *Croat 11878* (MO); 140 m, 9°06′20″N, 79°37′20″W, *Croat & Zhu 77072* (MO); Pipeline Road, 2–4 mi. N of Gamboa, ca. 100 m, *Gentry 6543* (MO); Río Cocoli, road K-9, *Stern et al. 348* (GH, MO, US); Paraíso, *Tyson & Lazor 6194* (F). **Coclé**: Penonomé and vic., 50–1000 ft., *Williams 381* (NY). **Darién**: Cerro Pirre region, El Real, *Croat & Porter 15460* (MO); Santa Fe region, Univ. of Georgia Cuipo Forest Site #2, 15 m, *Duke 14258* (F, MO). **Herrera**: Ocú, *Ebinger 1090* (MO, US). **Los Santos**: ca. 5 m S of Las Tablas, *Burch et al. 1236* (MO, UC); Pocrí, *Dwyer 1189A* (MO); Las Tablas, *Dwyer 1189* (MO). **Panamá**: along road to Bique, 5 km SW of Arraiján, 20–40 m, *Nee 7699* (MO, US); Panamá Viejo, *Rose 18505* (NY, US); road K-15 near Huile, vic. Gatún Lake, *Smith et al. 3277* (F, US); El Llano–Chepo, *Gentry & Tyson 1727* (MO, SCZ); Tocumen, *Dwyer 4220* (MO); vic. Macambo, *Croat 14911* (MO); Cerro Campana, *Croat 12018* (MO, SCZ); Penonomé and vic., 50–1000 ft., *Williams 381* (NY); San José Island, Pearl Archipelago, *Erlanson 234* (US); *402* (GH, US); *Johnston 974* (GH, MO), *918* (GH), *12* (GH), *960* (GH).

Philodendron jefense Croat, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, along road short of summit, 550–800 m, 9°15′04″N, 79°30′04W, *McPherson 10038* (holotype, MO–3475849; isotypes, K, PMA, US). Figures 238, 239.

Planta hemiepiphytica; internodia brevia, in sicco usque 3 cm diam.; cataphylla 20–24 cm longa, acute 2-costata, mox decomposita et persistentia ut fibrae pallide brunneae; petiolus teres, 38–76 cm longus, 4 mm

diam.; lamina late ovata, 39–54 cm longa, (22.5)34–49 cm lata, cordata basi, in sicco canoviridis; inflorescentia 1; pedunculus 10–13 cm longus, 4–5 mm diam.; spatha 9.5–14 cm longa, omnino viridis, in sicco cum magnis maculis albis; pistilla (6)7–8-locularia; locules cum 6 seminibus; baccae albae.

Hemiepiphytic; stem appressed-climbing; internodes short, to 3 cm diam.; roots moderately few per node, drying to 3 mm diam., sharply ridged, brown; cataphylls 20–24 cm long, sharply 2-ribbed, persisting, promptly weathering to light brown, semi-organized fibers with small, thin fragments of epidermis persisting; **petioles** 38–76 cm long, 4 mm diam., terete, drying black; **blades** broadly ovate, short acuminate at base, cordate at base, 39–54 cm long, (22.5)34–49 cm wide (0.8–1.4 times longer than wide), (0.5–0.6 times the petiole length), about one-half as long as the petiole, margins sinuate, upper surface glossy, drying gray-green and semiglossy, lower surface glossy, drying minutely granular; anterior lobe 22–25 cm long, 24.5–29.7 cm wide (1.8–2 times longer than posterior lobes); posterior lobes 12–14 cm long, 12.2–13.2 cm wide, obtuse; midrib drying darker than surface above; basal veins 5 pairs per side, first and second free to base, the remainder coalesced 3–6 cm; posterior rib naked to 3–3.5 cm long; primary lateral veins 5–6 per side, departing midrib at a 35–45° angle; minor veins frequently branched, arising from both the midrib and primary lateral veins, minute pustules visible between veins on both surfaces; "cross-veins" many. INFLORESCENCES 1 per axil; peduncle 10–13 cm long, 4–5 mm diam., terete, black-drying; **spathe** 9.5–14 cm long (ca. 1 time longer than peduncle), green throughout, drying with large white flecks; spathe blade 6 cm long; spathe tube 6 cm long; pistillate portion 5 cm long; **spadix** to 11 cm long; staminate portion 5.5–6 cm long, 7–10 mm diam.; fertile staminate portion to 1 cm diam.; sterile staminate portion 7 mm diam.; pistils 3.9 mm long; ovary (6)7–8-locular, locules 3.2 mm long, 0.4–0.5 mm diam., with axile placentation; ovules 2-seriate; funicle 0.3–0.4 mm long, adnate to lower part of partition, style similar to style type D; style apex flat; style boss small. INFRUCTESCENCE with berries white (immature); seeds 6 per locule, 1–1.1 mm long, 0.2–0.3 mm diam., translucent.

Flowering in *Philodendron jefense* is documented by a single collection with immature fruits collected in December. Flowering apparently occurs during the wet season.

Philodendron jefense is endemic to Panama on Cerro Jefe in *Premontane rain forest* at about 800 m elevation.

Philodendron jefense is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Reticulata.* This species is distinguished by its appressed-climbing habit, short, thick internodes, sharply 2-ribbed cataphylls promptly weathering to light brown, semi-organized fibers with small, thin fragments of epidermis persisting, terete petioles (about twice as long as the blades), broadly ovate, gray-green-drying blades, and solitary long-pedunculate inflorescences with the spathes green outside.

Philodendron jefense is probably closest to *P. lazorii* Croat, which shares broadly ovate, gray-green-drying leaf blades and semi-organized, brownish masses of persistent cataphyll fibers. The latter species differs in having matte-drying blades with the lower surface smooth and minutely brownish- or whitish-speckled, with the minor veins drying darker than the surface and weakly puckered without any sign of branching or cross-veins. In contrast, *P. jefense* has blades semiglossy on drying with the lower surface sparsely granular with frequently branched minor veins and with cross-veins not drying darker than the surface. The upper surface lacks any signs of raphide cells.

The species name refers to the type locality, Cerro Jefe, which has proven to be one of the most endemic-rich areas for its size of any site in Panama.

Philodendron jodavisianum G. S. Bunting, Gentes Herb. 9: 337. 1965. TYPE: Mexico. Chiapas: Cerro de Madrugal, along Teapa–Tacotalpa (Tabasco) Highway, at km 4, W of hwy., on rock face of steep slopes, *Bunting 1526* (holotype, US). Figures 243, 245–248, 253.

Usually hemiepiphytic, terrestrial; stem appressed-climbing, gray-green to brown or green, sap sweet-scented, drying blackened, leaf scars conspicuous, 2 cm long, 1.7 cm wide; internodes weakly flattened on one side, 2-ribbed, weakly glossy, to 8 cm long, but surely longer than wide and 2.5–3 cm diam. at apex, dark to medium green, soon gray, epidermis brown, flaking, fissured sometimes; roots whitish, few per node; cataphylls 10–20 cm long, bluntly or sharply 2-ribbed or unribbed, sharply D-shaped, somewhat spongy, light to medium green or reddish to brownish, sometimes streaked pinkish, semiglossy, drying brown, persisting semi-intact as pale fibers at upper nodes, disorganized below; **petioles** (18)29–91 cm long, (2)3–7(8–12) mm diam., sometimes terete, usually D- or U-shaped, spongy or firm, dark green, flattened or somewhat sulcate to convex, often with medial rib, margins raised adaxially, rounded abaxially, surface semiglossy, minutely and short-lineate; **blades**

triangular-ovate, ± subcoriaceous, moderately bicolorous, long acuminate at apex, deeply cordate at base, 25–74 cm long, 18–34 cm wide (1.1–2.8 times longer than wide), (0.5–2 times longer than petiole), broadest ± near the middle, upper surface dark green, drying blackish, semiglossy, lower surface pale green to yellow-greenish, drying blackish, glossy to semiglossy or matte; anterior lobe 18–58 cm long, 10.1–40.4 cm wide (1.7–4.3 times longer than posterior lobes); posterior lobes 8–17 cm long, (3.7)5–17 cm wide, obtuse to rounded; midrib broadly sunken to broadly convex or flat, dark green above, raised to narrowly convex, thicker than broad, concolorous or darker than surface below; basal veins 5–10 per side, in part coalesced to 4 cm, barely naked or naked to 2 cm; primary lateral veins 7–11 per side, departing midrib at a 50–60° angle, ± straight to the margins, obtusely to weakly or narrowly sunken and sometimes weakly quilted above, convex and darker than surface below; interprimary veins almost as prominent as primary lateral veins; minor veins in part discontinuous and darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2–6 per axil; peduncle 3–13 cm long (to 20 cm long in South America), 2–6 mm diam., pale green to whitish, with raised, prominent white striations; **spathe** semiglossy, 6–14.5 cm long (0.9–3 times longer than peduncle), sometimes greenish with short white lineations throughout; spathe blade white to pale green (at anthesis), reddish (post-anthesis) (B & K red-purple 7.5/7), short-lineate outside (opening 4.6 cm long, 3.6 cm wide), very pale green to white, matte, few, sparse, dark-lineate inside; spathe tube semiglossy and greenish to greenish brown or reddish (maroon or reddish at anthesis) outside, green to white inside; **spadix** weakly exserted from the spathe, 7.6–9.2 cm long, constricted near base of fertile staminate portion; pistillate portion pale green or whitish, cylindrical, 1.4–2.4 cm long, 1 cm diam. at apex, 1.1 cm diam. at middle; staminate portion 5.3–7.6 cm long; fertile staminate portion creamy white, cylindrical to weakly tapered, 0.85–1.5 cm diam. at base, 0.7–1.3 cm diam. at middle, 6–10 mm diam. ca. 1 cm from apex, broadest at the base, narrower than the pistillate portion, narrower than the sterile portion; sterile staminate portion broader than the apical area of the pistillate portion, gray-white, 1.1–1.5 cm diam.; pistils 1.8–2.5 mm long, 1–1.4 mm diam.; ovary 4–6(5–7)-locular; locules 1.3–1.7 mm long, 0.5–0.7 mm diam., with axile placentation; ovules 18–26(23–28) per locule, 2-seriate, 0.2–0.4 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition, style 0.2–0.3 mm long, 1–1.4 mm diam., similar to style type B; style apex flat to slightly rounded; stigma subdiscoid, brushlike, unlobed, 1–1.3 mm diam., 0.2–0.6 mm high, covering entire style apex; the androecium truncate, margins 4–6-sided; thecae oblong to obovate, 0.3–0.5 mm wide, ± parallel to one another, contiguous; sterile staminate flowers blunt, 1.6–1.8 mm long, 1.4–1.5 mm wide. INFRUCTESCENCE with berries white (mature), 6 mm long, 2.6 mm diam.; seeds 14–16(24–28) per locule, 1.3–1.7 mm long, 0.2–0.3 mm diam. JUVENILE plants with internodes 8 cm long, 5 mm diam.; petioles sharply U-shaped in cross section, usually lacking medial rib adaxially, margins erect.

Flowering in *Philodendron jodavisianum* occurs in the late dry season and throughout much of the rainy season (April through October) in Panama. In Costa Rica it has been collected in flower in February, and post-anthesis collections have been made in January. Immature fruits have been collected August through November.

Philodendron jodavisianum ranges from southern Mexico to Colombia, Ecuador, and Venezuela (Mérida) from near sea level to 1500 m elevation. It occurs in *Tropical wet forest* and *Premontane wet forest* in Panama and Costa Rica but also in *Tropical moist forest* in some parts of Central America.

Philodendron jodavisianum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is characterized by its short internodes, sharply 2-ribbed cataphylls persisting as pale fibers, petioles flattened or somewhat sulcate above and usually with a medial rib, usually triangular-ovate, blackish-drying blades with many impressed primary lateral veins, and spathes usually greenish on the tube and white on the blade.

Philodendron jodavisianum is quite variable throughout its range, and the type (being one of the most northerly collections) differs from most in having more elliptic blades.

Philodendron jodavisianum is most easily confused with *P. grandipes*, which differs in comprising terrestrial plants with broadly ovate leaf blades. It has also been confused with *P. panamense* K. Krause, which differs in having subterete petioles, promptly deciduous cataphylls, and longer peduncles often bent beneath the spathe (see *P. panamense* for additional details).

Similar collections from South America, especially *Croat 57441* from Bahía Solano, Chocó Department, Colombia, differ in sometimes having distinct "cross-veins." Collections from Pichincha Province, Ecuador (*Croat 55737* and *Grayum & Zamora 9431*), differ in having peduncles 16–20 cm long.

Two Darién collections (*Hammel et al. 16252* and *McPherson 11517*) are unusual in having leaf blades with somewhat flaring posterior lobes and markedly

concave margins. However, the leaves on the second sheet of the McPherson collection are typically shaped with a convex blade margin.

Additional specimens examined. BELIZE. **Toledo**: Blue Creek, *Whitefoord 3234* (BM). COSTA RICA. **Alajuela**: Los Ensayos, Buena Vista de San Carlos, *Barquero 10* (UC); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, ca. 850 m, *Croat 43583* (MO); Reserva Biológica Monteverde, along Río Peñas Blancas, 820 m, 10°21′N, 84°40′W, *Bello & Haber 2881* (INB, MO); Río Zapote, 5 km S of Canalete, along new road to Upala, 100–200 m, 10°48′N, 85°02′W, *Burger & Baker 9961* (F, MO, SEL); Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36279* (MO); San Ramón, *Bittner & G. Herrera 2134* (CR). **Cartago**: Moravia–Quebrada Platanillo, Moravia, 3–5 km from Finca Racine, 1200–1300 m, *Croat 36648* (MO); along Camino Raiz de Hule, SE of Platanillo, 1200–1400 m, *Croat 36756* (MO); Jicotea Valley, Jicotea–Río Pacuare, *Croat 36539* (MO). **Guanacaste**: slopes of Miravalles, above Bijagua, ca. 1500 m, *Gómez 19048* (MO). **Heredia**: 11 km E of Cariblanco, 1060 m, *Loiselle 255* (MO); Paracito–Río Claro, Bajo La Hondura, 1100–1400 m, *Croat 44516* (MO); Parque Nacional Braulio Carillo, 1000 m, 10°16′38″N, 84°04′57″W, *Boyle 1285* (MO); Zona Protectora "La Selva," along trail from main road across Quebrada Cantarrana to Río Guácimo, 300 m, *Grayum & Schatz 3216* (DUKE); La Selva Field Station, ca. 100 m, *Croat 44300* (MO); 100–150 m, *44320* (MO); *Grayum 1915* (MO); *Jiménez V* (MO); *Murrell 1710* (DUKE); Río Frío, W of Finca Zona Nueve, ca. 110 m, 10°18′N, 83°53′W, *Grayum 3562* (MO); Río Sucio, near Puerto Viejo, 2 m, *Croat 35703* (MO). **Limón**: Manzanillo de Talamanca, ca. 5 m, 9°38′N, 82°39′W, *Grayum & Burton 4340* (MO); ca. 11 mi. S of Siquirres, 650 m, *Croat 43329* (MO); Cerro Coronel, 10–40 m, 10°40′N, 83°40′W, *Stevens 24346* (MO); Río Sixaola, ca. 0.5 mi. SW of Bambú, ca. 3 mi. NE of Bratsi, ca. 15 m, *Croat 43254* (MO). **Puntarenas**: ca. 1 km S and 2 km W of Cañasas, 60 m, 8°34′N, 83°25′W, *Croat & Grayum 59807* (CM, CR, K, MO); Osa Península, 200 m, *Aguilar 2201* (CR, INB); Golfo Dulce Forest Reserve, Rancho Quemado, 200 m, 8°42′N, 83°33′W, *Hammel & Robles 16834* (CR, MO); Piedras Blancas, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67696* (CR, MO); *67693* (CR, F, MO); Golfito, *G. Herrera & Rivera 7042* (CR). **San José**: above Río Sucio, 5–6000 m, *Pennington et al. 11529* (K); San Isidro del General–Dominical, SW of San Isidro, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35253* (CR, F, MO); 9 mi. SW of Río Pacuar, 680 m, *Croat 35344* (MO); Carara Reserve, SW part of Montañas Jamaica, ca. 2.5 km NE of Bijagual de Turrubares, 460–520 m, 9°45′N, 84°33′30″W, *Grayum et al. 5488* (MO); vic. of San Isidro El General, 900 m, *Molina et al. 18063* (EAP, F, GH, NY, UC, US); Puriscal, Z.P. La Cangreja, 800 m, *Morales 2020* (CR, INB); Tarrazú, vic. Hormiguero, 1100–1200 m, *Croat 78962* (INB, MO). GUATEMALA. **Alta Verapaz**: Tucurú–El Estor, 4–9 mi. up road to Oxec, gravel road N off Hwy. 7E, ca. 6 km NE of Panzós, 500–800 m, *Croat 41607* (MO); *41698* (K, MO, NY). **Izabal**: 12 km NW of El Estor, 650 m, *Martínez & Stevens 23305* (MO). HONDURAS. **Atlántida**: Lancetilla Botanical Gardens, 2 mi. WSW of Tela, 10–150 m, *Croat 42640* (K, MO); 70–90 m, 15°44′N, 87°27′W, *Croat & Hannon 64612* (CM, CR, EAP, G, MEXU, MO); Lancetilla, 100 ft., *Yuncker 5008* (F, MICH, MO, NY). MEXICO. **Tabasco**: Mpio. Teapa, 7 km SE of Teapa on road to Tacotalpa, Rancho San Eneas, 70 m, 17°35′N, 92°50′W, *Hammel & Merello 15516* (MO). NICARAGUA. **Chontales**: 4 km NNW of Cuapa, Cerro Oluma, 700–775 m, 12°18′N, 85°23′30″W, *Nee 28413* (MO, NY). **Río San Juan**: Caño Chontaleño, 20 km NE of El Castillo, 200 m, *Neill & Vincelli 3623* (MO); Río Indio, 5 hours upriver from San Juan del Norte, 11°07′N, 83°50–52′W, *Riviere 247* (MO). **Zelaya**: ca. 6 km upriver from Barra de Punta Gorda, 8–10 m, 11°30′N, 83°49′W, *Stevens 20756-a* (MO); Mpio. Siuna, Santa Rosa, *Ortiz 67* (MO). PANAMA. **Bocas del Toro**: Escudo de Veraguas Island, N coast, 5 m, 9°05′N, 81°35′W, *McPherson 11412* (MO, US); Fortuna Dam area, road along Continental Divide, 2.8 mi. S of Continental Divide, 850–950 m, 8°45′N, 82°15′W, *McPherson 9676* (MO, US); Chiriquí Grande–Fortuna, 1.2 mi. N of Divide, 5.3 mi. N of bridge over Fortuna Dam, 910 m, 8°44′N, 82°17′W, *Croat 60450* (MO, PMA, RSA); along Divide, 1.1 mi. W of highway, 1200 m, 8°44′N, 82°17′W, *Croat 60368* (MO); E of camp Corriente Grande (IRHE), 200 m, *Correa et al. 3697* (PMA). **Chiriquí**: Río Chiriquí Valley, vic. of Fortuna Dam, 1100–1200 m, 8°45′N, 82°18′W, *Croat 66587* (F, IBE, M, MEXU, MO, US); 1000–1200 m, 8°45′N, 82°15′W, *Correa et al. 2686* (MO, PMA); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60080* (CM, MO); Gualaca–Fortuna, 10 mi. NW of Los Planes de Hornito, 1260 m, 8°45′N, 82°17′W, *Croat 50074* (MO); Gualaca–Chiriquí Grande, Río Hornito, ca. 0.5 km S of Centro de Científicos, 1010–1130 m, 8°44′N, 82°13′30″W, *Croat 67922* (MO); 8°45′N, 82°18′W, *Croat & Zhu 76376* (MO, SEL); 1100–1200 m, 8°45′N, 82°15′W, *Thompson 5026* (CM); Río Chiriquí, beyond Gualaca, 10.8 mi. beyond Los Plantes de Hornito, ca. 1400 m, *Croat 48721* (MO). **Coclé**: Santa Rita Ridge Road, 4–6 km from Transisthmian Highway, 150–200 m, *Croat 34280* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76960* (MO); El Copé region, near Continental Divide, ca. Mile 1.5, ca. 900 m, *Croat 44572* (MO); ca. Mile 5.6, 800 m, *Croat 75068* (MO); La Pintada–El Copé, 3000 ft., *Hammel 2633* (MO); El Valle region, N of El Valle de Antón, La Mesa, 900–1000 m, 8°40′N, 80°10′W, *Hamilton et al. 4111* (INB, MO); 800–900 m, 8°38′N, 80°09′W, *Croat 67122* (CAS, CM, COL, HNMN, L, MEXU, MO, PMA); 860–900 m, *37396* (MO); *67211* (AAU, DUKE, MO, NY, PMA, TEX); *67213* (AAU, CM, EAP, MO, PMA, TEX, USCG); *67121* (F, HNMN, MO); *67129* (AAU, CAS, CM, COL, CR, F, HUA, K, L, MEXU, MO, NY, P, PMA, SEL, TEX); 775 m, 8°36′N, 80°07′W, *74793* (KUN, MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76742* (MO, SEL); *76710* (MO). **Colón**: Río Guanche, ca. 3–5 mi. inland, 10–100 m, *Croat 26175* (MO). **Darién**: Cerro Pirre region, Alturas de Nique region, S of El Real, near Cana mine, 650–800 m, 7°45′N, 77°40′W, *McPherson 11526* (MO); *11517* (B, MO); Cana gold mine, 480 m, *Croat 38003* (MO); *38039* (MO); 600–100 m, *Croat 37743* (MO); Parque Nacional Darién, N of Tacarcuna, ca. 18 km E of Pucuro, 600–800 m, 8°05′N, 77°16′W, *Hammel et al. 16481* (MO); ca. 17 km E of Pucuro, 850 m, 8°03.5′N, 77°17′W, *16252* (MO). **Panamá**: El Llano–Cartí road, 10 m from highway, near El Llano, 330 m, *Croat 33779* (F, MO, NY); Mile 5–6, 350–375 m, *34771* (F, MO); Mile 6.8, 350 m, *49128* (AAU, CAS, CM, MEXU, MO); Mile 10.1, 325–350 m, *67366* (MO); Río Majé–Quebrada Brava, ca. 60 m, *Croat 34657* (F, MO); Cerro Campana, *Croat 25252* (MO); *25204* (MO); along trail to summit, 780–875 m, *Croat 17207* (F, MO, NY); at end of road beyond Su Lin Hotel, *Croat 14227* (MO); 800 m, 8°41′N, 79°56′W, *74772* (CM, MO); summit and upper trail, *Witherspoon & Witherspoon 8462* (MO); ca. 1 mi. from highway, 450 m, *Croat 35950* (MO, PMA); Cerro Jefe region, Campo Tres, ca. 700 m, *Croat 27064* (F, MO); 700–750 m, 9°15′N, 79°25′W, *Croat 68687* (IBE, MO, TEX). **San Blas**: El Llano–Cartí, 23–29 km from Pan-American Highway, 300–400 m, 9°22′N, 78°69′W,

Knapp 1839 (MO, PMA); El Llano–Cartí Road, vicinity Nusagandi, 300–350 m, 9°15′N, 79°W, *Croat 69279* (DUKE, MO); 300 m, 9°20′N, 79°W, *Croat & Zhu 76542* (MO); 350 m, 9°20′N, 79°W, *Croat & Zhu 77011* (MO); 450 m, 9°18′N, 79°59′W, *Croat 75121* (MO). **Veraguas**: Río Concepción–Río Barrera, 300–600 ft., *Hammel 5252* (MO); Santa Fe region, Alto Piedra–Calovébora, 0.5 mi. N of Escuela Alto Piedra, Parque Nacional Cerro Tute, 800–1030 m, *Croat & Zhu 76914* (MO); 5–8 km from school, 730–770 m, *Croat 25967* (MO); Río Primero Brazo, 5 mi. NW of Santa Fe, 700–1200 m, *Croat 23114* (MO); 15.6 km NW of Santa Fe, 450–550 m, *Croat 27639* (MO); 0.6 mi. beyond Escuela Agrícola Alto Piedra, 730 m, *Croat & Folsom 33997A* (MO); *34062* (MO); ca. 1200 m, 8°32′N, 81°07′W, *Hamilton et al. 1280* (MO); Escuela Agrícola Alto Piedra, *Mori & Kallunki 2529* (MO); Santa Fe–Río San Luis, past Escuela Agrícola Alto Piedra, Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66901* (CM, MO).

Philodendron knappiae Croat, sp. nov. TYPE: Panama. Chiriquí: Cerro Hornito, in elfin forest on ridges and summit, approached from Los Planes de Hornito, 2100 m, 8°42′N, 82°06′W, 14 Mar. 1982, *Knapp, Kress & Hammel 4219* (holotype, MO–3043611). Figures 240, 244, 249, 254.

Planta terrestris aut hemiepiphytica; internodia 0.5–7 cm longa, 1–1.7 cm diam., in sicco brunnea; cataphylla 10–18 cm longa, acute 2-costata, sulcata adaxialiter, viridia, decidua; petiolus obtuse D-formatus, 14–19 cm longus, in sicco 2–7 mm diam.; lamina ovato-triangularis, cordata basi, 16–23.5 cm longa, 7.5–11.5 cm lata; inflorescentia 1; pedunculus 2–3 cm longus, 5–6 mm diam.; spatha 7–8 cm longa, extus viridis, intus subrosea; pistilla 4-locularia; loculi 4-ovulati.

Terrestrial or hemiepiphytic; stems usually erect; internodes short, somewhat flattened on one side with marginal ribs, moderately glossy, 0.5–7 cm long, 1–1.7 cm diam., longer than broad below, short near apex, medium green, epidermis smooth, light brown; cataphylls 10–18 cm long, sharply 2-ribbed, green, sulcate adaxially, margins weakly raised abaxially, deciduous; **petioles** 14–19 cm long, 2–7 mm diam., bluntly D-shaped, green, tinged reddish; **blades** ovate-triangular, subcoriaceous, bicolorous, long-apiculate at apex, cordate at base, 16–23.5 cm long, 7.5–11.5 cm wide (1.8–3 times longer than wide), (1.1–1.4 times longer than petiole), about equal in length to petiole, upper surface semiglossy, drying dark brown, lower surface slightly paler, drying dark yellow-brown or dark yellow-green; anterior lobe 12–18.5 cm long, 10.6–13 cm wide (2.2–3.3 times longer than posterior lobes); posterior lobes 5–8 cm long, 5–6.5 cm wide (1.4–1.8 times longer than wide), narrowly to obtusely rounded; sinus hippocrepiform, 3–5.5 cm deep; midrib broadly convex, paler than surface above, convex, reddish or paler than surface below; basal veins 3(5) per side, with 0–1 free to base, 2–3 coalesced 1–1.5 cm; posterior rib naked; primary lateral veins 5–7 per side, departing midrib at a (40)55–70° (lowermost to 80°) angle, arcuate-ascending to the margins, weakly visible above, weakly raised, often reddish below; minor veins distinct below, arising from the midrib only; secretory ducts present but inconspicuous. INFLORESCENCES 1 per axil; peduncle 2–3 cm long, 5–6 mm diam.; **spathe** 7–8 cm long (2.3–3.6 times longer than peduncle), weakly constricted above the tube, 1.5 cm diam. at constriction, green throughout, pinkish within; spathe tube 3–4 cm long, 1.9 cm diam.; **spadix** 5.5–7 cm long, white throughout; pistillate portion 1.2 cm long, 1 cm diam.; staminate portion 4.3–5.8 cm long, 8–12 mm diam.; pistils 1–1.3 mm long, 0.7 mm diam.; ovary 4-locular; locules 0.8 mm long, 0.3–0.4 mm diam., with axile placentation; ovules 4 per locule, 2-seriate, 0.2 mm long, longer than funicle; funicle 0.1 mm long, adnate to lower part of partition, style similar to style type B; style apex flat to concave; stigma ± hemispheroid, unlobed, 0.8 mm diam., 0.2 mm high, covering entire style apex; the androecium truncate, ± prismatic, margins irregularly 4–6-sided, mostly 4–5-sided, 0.8–1.1 mm long; thecae oblong, 0.4 mm wide, ± parallel to one another, not contiguous; sterile staminate flowers irregularly 4–6-sided, 0.9–1.1 mm long.

Flowering in *Philodendron knappiae* apparently occurs in the dry season and is documented by only two fertile collections, one flowering and one post-anthesis, both made in March.

Philodendron knappiae is endemic to western Panama, known only from the type locality in Chiriquí Province on Cerro Hornito in *Tropical Lower Montane rain forest* at 2100 m elevation.

Philodendron knappiae is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is recognized by its relatively small stature; short internodes (distally) with smooth, brown epidermis; adaxially sulcate, sharply two-ribbed, green but densely short-red-lineate, deciduous cataphylls; bluntly D-shaped petioles (about as long as the blades); small, ovate-triangular dark brown-drying blades with a hippocrepiform sinus; and solitary inflorescences with the spathe green outside and pink inside.

The species is perhaps most easily confused with *P. wilburii*, which has leaf blades of similar size and shape. The latter species differs in having longer internodes drying with a tan, glossy epidermis, thicker blades drying yellowish green to dark olive brown above, 2–3 inflorescences per axil, and 2 ovules per locule (vs. 4 per locule for *P. knappiae*).

Additional specimens examined. PANAMA. **Chiriquí**: Cerro Hornito, above Los Planes de Hornito, 1750 m, 8°41′N, 82°10′W, *Croat 67982* (CM, MO); 2100 m, *Kress et al. 82-1363* (DUKE).

Philodendron lazorii Croat, sp. nov. TYPE: Panama. Canal Area: vic. Madden Lake, along both sides of stream SSE of pumping station (SE of dam), 140 m, 9°13′N, 79°37′W, 18 Jan. 1990, *Croat 69833* (holotype, MO–3789003–5; isotypes, AAU, B, CAS, CM, COL, CR, F, GH, K, MEXU, NY, PMA, QCNE, RSA, SCZ, TEX, US, VEN). Figures 13, 14, 250–252, 255–258.

Planta hemiepiphytica; internodia 1–4 cm longa, 5 cm diam.; cataphylla acute D-formata, persistentia semi-intacta nodis superioribus, demum decidua; petiolus teres, 37–63(76) cm longus, 5–6 mm diam.; lamina late ovata, 32–54 cm longa, (22)34–49 cm lata, cordata basi, in sicco canoviridis; sinus hippocrepiformis vel obovatus; inflorescentia 2; pedunculus 8.6–17 cm longus; spatha 12–13.5 cm longa; pistilla (4)5–6-locularia; loculi 10–14(18)-ovulati.

Hemiepiphytic; stem appressed-climbing (scandent as juvenile); internodes weakly striate, 1–4 cm long, 5 cm diam., ± broader than long, light olive-green to dark yellow-green, glossy, roots 1–3 per node, dark brown to reddish brown, matte, smooth to densely scaly, to 30 cm or longer, 3–5 mm diam., feeder roots to 8 mm diam., densely scaly; cataphylls 17–19 cm long, pale yellow-green, sharply D-shaped, margins acutely raised, persisting semi-intact at upper nodes with a dense reticulum of coarse fibers, often overlain with a thin, fragmented epidermis, becoming dilacerated, eventually deciduous; **petioles** 37–63(76) cm long, 5–6 mm diam., terete, dark green, firm, flexible, surface matte, faintly dark green striate; **blades** broadly ovate, subcoriaceous, long-acuminate at apex, cordate at base, 32–54 cm long, (22)34–49 cm wide (0.97–1.4 times longer than wide, averaging 1.13 times), (0.65–0.9 times the petiole length), slightly shorter in length than petiole, upper surface dark green, drying gray-green, weakly to semiglossy, lower surface drying gray-green, matte, much paler; anterior lobe 27–33 cm long, 36 cm wide (1.6–2.2 times longer than posterior lobes); posterior lobes 13–17 cm long, 16–19.5 cm wide, obtuse; sinus hippocrepiform to obovate, 9.5–11.5 cm deep; midrib flat to broadly raised, concolorous to slightly paler than surface above, narrow-rounded to bluntly acute, darker than surface below; basal veins (5)6–7 per side, with 0–1 free to base, 3rd and higher order veins coalesced 2–4.5 cm, obscure; posterior rib 2–3 cm long along the sinus; primary lateral veins 3–4 per side, departing midrib at a 40–50° then to 70° angle, straight to weakly arcuate to the margins, weakly and obtusely sunken and concolorous or paler above, convex and darker than surface below; minor veins moderately distinct, arising from both the midrib and primary lateral veins, drying weakly puckered and darker than surface below, upper surface usually drying with whitish cells visible, lower surface drying smooth and minutely brownish to whitish speckled. INFLORESCENCES 2 per axil; peduncle 8.6–17 cm long, to 1.1 cm diam., medium green, lightly white-striate, heavily white-striate nearest apex; **spathe** 12–13.5 cm long (spathe equal in length to or slightly shorter than peduncle), constricted above the tube, 2.9 cm diam. at constriction, margins pale to creamy; spathe blade yellowish green outside, 8 cm long (opening 4 cm wide), creamy on outer margins, glossy inside; spathe tube medium green, finely white-striate with pale margins outside, 5 cm long, 3.3 cm diam., pale yellowish green, glossy inside; **spadix** bluntly pointed at apex, 10.9–11.3 cm long, constricted 1.5 cm above base of fertile staminate portion; pistillate portion pale yellowish green, 3.3–4 cm long, 1 cm diam. at base, 1.5 cm diam. midway, 1.4 cm diam. at apex; staminate portion 7.8–9.3 cm long; fertile staminate portion creamy white, 1.7 cm diam. at middle, 11 mm diam. ca. 1 cm from apex; sterile staminate portion barely detectable, creamy white, drying darker than fertile staminate flowers, 1.7 cm diam.; pistils 1.9–2.5 mm long; ovary (4)5–6-locular, 1.1 mm diam., locules 1.1–1.6 mm long, 0.3–0.4 mm diam., with axile placentation; ovules 10–14(18) per locule, 2-seriate, 0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition, style 0.9 mm diam., similar to style type D; style apex ± rounded to bluntly pointed; style boss broad and pronounced; stigma subdiscoid, unlobed, ± truncate, 1.5 mm diam., 0.3 mm high, covering entire style apex, depressed shallowly and medially; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 0.7–1 mm long; thecae oblong, 0.4–0.5 mm wide, not contiguous, ± parallel to one another; sterile staminate flowers irregularly 4–6-sided, slightly clavate to prismatic, 1.2–1.9 mm long. JUVENILE plants with internodes matte, gray-green, 6 cm long, 7 mm diam.; petioles terete; blades weakly velvety; upper surface ± glistening-glossy, lower surface matte, much paler, with flecks of brilliance; minor veins very distinct, darker than surface.

Flowering in *Philodendron lazorii* occurs in the late dry season and early rainy season (March through June), with mature fruits in August. Immature fruits have been collected in March and June, which indicates that there must be flowers in the late wet season as well (or perhaps it indicates bimodal flowering).

Philodendron lazorii is endemic to Panama, known from the type locality, a region of limestone outcrops near Madden Lake, at about 100 m elevation in *Tropical moist forest*, and in Darién Province at 250 to 1050 m in *Tropical moist forest* and *Premontane wet forest.*

Philodendron lazorii is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its thick, short internodes, cataphylls persisting semi-intact with an organized network of yellow-brown fibers, terete petioles averaging 1.25 times longer than the blade, and broadly ovate, gray-green-drying blades matte on the lower surface.

Philodendron lazorii is probably most closely related to *P. panamense,* which has similar inflorescences. The latter species differs in having semiglossy, ovate-triangular blades usually 1.3 or more times longer than wide (averaging 1.5 times longer than wide), and petioles commonly shorter than the blade. In addition, it has generally shorter peduncles (usually shorter than the spathe).

This species is also similar to *P. jefense.* See that species for a discussion of the differences.

Philodendron lazorii is named in honor of one of its original collectors, Robert Lazor (Army Corps of Engineers, Vicksburg), who collected in Panama while a student at Florida State University.

Additional specimens examined. PANAMA. **Canal Area**: Madden Lake Cave area, ca. 9°13′N, 79°37′W, *Tyson & Lazor 6266* (FSU, IBE); Salvador Hill, near Juan Mina, *Bartlett & Lasser 16785* (MICH, MO). **Darién**: along trail from base camp to Rancho Frío on slopes of Cerro Pirre, 200–450 m, 7°58′N, 77°43′W, *Croat & Zhu 77126* (CAS, CM, CR, MO); W side of Cerro Pirre, 800–1050 m, 7°56′N, 77°45′W, *Croat 68953* (DUKE, HUA, M, MO).

Philodendron lentii Croat & Grayum, sp. nov. TYPE: Panama. Coclé: El Valle region, between Finca Mandarinas and Finca Furlong, ca. 1 km off road, vic. La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, 11 June 1987, *Croat 67163* (holotype, MO–3582921; isotypes, AAU, B, BR, CAS, CM, COL, CR, CUVC, DUKE, EAP, F, G, GH, HMNM, HUA, IBE, K, MEXU, NY, P, PMA, QCA, RSA, S, SCZ, TEX, US, VEN). Figures 259–265.

Planta hemiepiphytica; caulis scandens; internodia 4–12 cm longa, 1.5–4.5 cm diam.; cataphylla 20–23(40) cm longa, plerumque incostata, interdum 1–2 costata, decidua; petiolus teres vel late D-formatus, interdum late sulcatus, 22–44 cm longus, 4–12 mm diam.; lamina ovato-cordata, 21.6–51 cm longa, 9–25 cm lata, truncata vel subcordata basi; nervis basalibus 1–3(4) utroque, liberis basi; inflorescentia 1–2; pedunculus 3–10 cm longus; spatha 12–21 cm longa, lamina spathae extus viridalba vel alba, intus atrimarronina vel creamea; tubo spathae extus albo vel viridalbo, interdum suffuso subroseo, intus atrimarronino vel violaceipurpureo; pistilla (5)6–8-locularia; loculi (1–2)4–6-ovulati; baccae aurantiacae.

Hemiepiphytic; stem scandent, creeping, assurgent, sap soapy-scented; internodes elongate, semiglossy to matte, 4–12 cm long, 1.5–4.5 cm diam., usually slightly longer than broad, medium to dark green, conspicuously pale striate at upper edge of each node, drying brownish, often narrowly ribbed (ribs irregularly ridged, sometimes warty), epidermis weakly fissured transversely; roots moderately few, to ca. 30 cm long, drying to 2 mm diam., reddish brown; cataphylls 20–30(40) cm long, usually unribbed, sometimes 1-ribbed, sharply 1-ribbed, or weakly to sharply 2-ribbed, greenish, tinged reddish, deciduous, intact; **petioles** 22–44 cm long, 4–12 mm diam., terete to broadly D-shaped, firm, dark green, sometimes purplish below, broadly sulcate, flattened or broadly convex adaxially, convex abaxially, with adaxial margins obtuse to rounded, surface semiglossy, densely and minutely white or dark striate-lineate; **blades** ovate to narrowly ovate or ovate-elliptic, coriaceous to subcoriaceous, conspicuously bicolorous, acuminate to narrowly acuminate at apex, rounded to truncate or subcordate at base, 21.6–51 cm long, 9–25 cm wide (1.4–2.7(3.3) times longer than wide), (0.7–1.4(2.25) times longer than petiole), usually about equal in length to petiole, upper surface dark green, semiglossy, drying dark grayish brown to yellowish brown, lower surface semiglossy to matte, paler; anterior lobe 28–45.5 cm long, 9–25 cm wide (4.9–10.2 times longer than than posterior lobes); posterior lobes 3–7 cm long, broader than long, broadly rounded to obtuse; sinus ± V-shaped to arcuate, to 4 cm deep; midrib flat to broadly convex, paler than surface above, convex, tinged reddish or darker than surface, drying minutely granular below; basal veins 1–3(4) per side, with all free to base; primary lateral veins 8–14 per side, departing midrib at a 60–70° angle, weakly arcuate, ascending to the margins, weakly to narrowly sunken or weakly quilted, drying paler than surface, raised along the margins with the center collapsed (forming a channel) above, convex to weakly raised or weakly pleated, darker than surface, drying minutely granular, paler than surface below; interprimary veins weakly sunken or obscure above, visible below; minor veins visible, few, darker than surface, arising from both the midrib and primary lateral veins, minutely etched in upper surface of fresh leaves, drying raised. INFLORES-

CENCES 1–2 per axil; peduncle 3–10 cm long, 3–7(14) mm diam., pale green; **spathe** 12–21 cm long (1.5–3.98(4.5–5.1) times longer than peduncle), margins reddish; spathe blade greenish white to white outside, 4 cm diam., dark maroon to cream inside; spathe tube white to greenish white, sometimes tinged pinkish or red, densely white-lineate outside, 6–9 cm long, dark maroon to violet-purple, densely white-lineate inside; **spadix** sessile; pale greenish to white throughout, cylindrical, tapered, 11–14(18) cm long, broadest near the base or slightly above the middle, constricted below the middle; pistillate portion green, cylindrical to ovoid-tapered, 6.6 cm long in front, 4.5 cm long in back, 1.1 cm diam. at apex, 1.3–1.4 cm diam. at middle, 8–11 mm wide at base; fertile staminate portion greenish white, tapered to clavate or cylindrical, 6.8–9.4 cm long, 9–16 mm diam. at base, 9–15 mm diam. at middle, 8–10 mm diam. ca. 1 cm from apex, broadest at or near the base, broader than the pistillate portion, sterile staminate portion not detectable; pistils 1.6–2.4 mm long, 1–1.8 mm diam.; ovary (5)6–8-locular; locules 1.2–2 mm long, 0.3–0.6 mm diam., ovule sac 0.8–1.5 mm long, with basal or sub-basal placentation; ovules (1–2)4–6 per locule, 1- or 2-seriate, 0.3–0.5 mm long, longer than or equal in length to funicle; funicle 0.1–0.4 mm long (can be pulled free to base); style 0.1–0.5 mm long, 1–1.6 mm diam., similar to style type B; style apex flat or weakly rounded; stigma discoid, brushlike, unlobed, 1–1.3 mm diam., 0.1–0.2(0.6) mm high, covering almost entire style apex or just the center of style apex; the androecium truncate, margins 4–6-sided (4–5-sided); thecae oblong, 0.3–0.5 mm wide, contiguous or ± parallel to one another; sterile staminate flowers 4–6-sided, 1.1–1.5 mm long, 0.8–1.3 mm wide. INFRUCTESCENCE with berries orange; seeds 3–4 per locule, 1–1.1 mm long, 0.5–0.6 mm diam.

Flowering in *Philodendron lentii* appears to occur during the dry season and early rainy season (February, March, June, and July). Post-anthesis collections exist from January, March through July, and November, indicating a somewhat broader range of flowering. Most post-anthesis inflorescences were collected between March through July. Immature fruits are known from January, April, and July while mature fruits are known from April, June, and July.

Philodendron lentii ranges from Costa Rica (Cartago) to Panama (Chiriquí to Coclé), from (210)670 to 1800 m elevation in *Premontane rain forest* and *Tropical Lower Montane rain forest* life zones. In Costa Rica, this species is apparently rare, having been collected only near Tapantí and Moravia in Cartago Province and near Cariblanco in Alajuela Province. In Panama, it has been collected mostly in the Fortuna Dam region, at Cerro Colorado (both Chiriquí), at Santa Fe in Veraguas and at El Valle and El Copé in Coclé Province.

Philodendron lentii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Ecordata.* This species is distinguished by its somewhat scandent habit; elongate internodes; deciduous cataphylls; D-shaped to broadly sulcate petioles (about as long as the blades); ovate, subcordate blades with the few basal veins free; and one to two large inflorescences with the spathe white externally and purplish internally on the tube. Also characteristic are the orange berries. Especially useful for recognition is the upper dried blade surface, which usually dries dark with the lateral primary and minor veins weakly raised.

Philodendron lentii may be confused with *P. heleniae,* which has blades of similar size and shape with few pairs of free basal veins and petioles about as long as the blades. That species differs in having more slender stems, subterete petioles, and several to many small, red inflorescences. Although a few collections of *P. lentii* (*Knapp 4970, Thompson 5022*) report the spathe to be red, these cannot be confused with *P. heleniae,* owing to the much larger size of the spathes (mostly more than 12 cm long vs. mostly less than 10 cm long for *P. heleniae*).

Possibly also belonging to this species is a sterile collection from Ecuador (Esmeraldas), *Croat 72298,* which differs in having internodes to 30 cm long, more numerous primary lateral veins (to ca. 20), and interprimary veins also sunken on live plants giving the blade the appearance of having very close primary lateral veins. This collection also differs in having the cross-veins prominulous on the lower surface toward the margin. Despite these differences, this Ecuadorian collection surely represents either *P. lentii* or another closely related new species.

Philodendron lentii is named in honor of Roy Lent, who first collected the species in 1967. Lent, a resident of Costa Rica, has been an important collector over many years and has collected many new species of Araceae.

Additional specimens examined. COSTA RICA. **Alajuela**: 3 mi. S of Cariblanco, 760 m, *Croat 35777* (MO). **Cartago**: Moravia–Quebrada Platanillo, Moravia, 3–5 km from Finca Racine, 1200–1300 m, *Croat 36592* (F, MEXU, MO, US); Río Grande de Orosi, 0.5 km W of Tapantí, 1200 m, *Lent 909* (CR, F). PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, near Continental Divide, 1170 m, 8°44′N, 82°17′W, *Croat 66647* (B, CAS, CR, K, MO, PMA, US); 1200 m, *60360*

(CAS, MO); 1.2 mi. N of Divide, 910 m, 8°44′N, 82°17′W, *Croat 60441* (K, MO, US). **Chiriquí**: Cerro Colorado, vic. of Cerro Colorado Copper Mine Development, 28 mi. above San Félix, 1200–1500 m, *Croat 33273* (MO); Cerro Pate Macho, ca. 5 mi. NE of Boquete, 1800–2200 m, *Croat 48567A* (MO); 1600–1700 m, 8°48′N, 82°23.5′W, *Grayum et al. 6358* (MO); vic. of Boquete, 1630–1780 m, 8°46′N, 82°25′W, *Croat 66395A* (MO); *66391* (MO); *66355* (CM, MO); Fortuna Dam area, 1100–1200 m, 8°45′N, 82°05′W, *Thompson 5022* (CM, MO); 8 km N of Los Planes de Hornito, 1250–1300 m, 8°45′N, 82°12′W, *Knapp 4970* (MO, NY); 11.8 mi. N of Los Planes de Hornito, 1400 m, *Croat 48682* (CM, MO); 10.8 mi. beyond Los Planes de Hornito, ca. 1400 m, *Croat 48712* (MO); 10.1 mi. NW of Los Planes de Hornito, 1250 m, 8°45′N, 82°17′W, *Croat 50041* (CM, MO); 10 mi. NW of Los Planes de Hornito, 1260 m, *Croat 50102* (MO, NY, PMA); Chiriquí Grande–Fortuna, 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60007* (K, MO, US); *60069* (K, MO, US); Gualaca–Chiriquí Grande, 8 mi. N of Los Planes de Hornito, 1.4 mi. W of Centro de Operaciones, along trail to Río Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67923* (CM, MO); near Fortuna Lake, 8°45′N, 82°18′W, *Croat & Zhu 76388* (MEXU, MO); N edge of lake, ca. 1100 m, ca. 8°45′N, 82°15′W, *McPherson 9078* (MO, NY); Fortuna Dam, 1200 m, *Hammel 2196* (MO); Quebrada Arena, 1050 m, 8°45′N, 82°16′W, *Hammel et al. 14706* (CR, MO); 26 km past Gualaca, 670 m, 8°35′N, 82°19′W, *Hoover 1329* (CAS, MO). **Coclé**: Penonomé–Coclecito, above Río Cascajal, 5.7 mi. N of Llano Grande, 210 m, 8°40′N, 80°26′W, *Croat 67538* (MO, PMA); El Copé region, Alto Calvario, Continental Divide, 5.2 mi. above El Copé, 930 m, *Croat 49204* (MO); Alto Calvario, 710–800 m, 8°39′N, 80°36′W, *Croat 68724* (MO); El Valle region, *Croat 14367* (MO); 2700 ft., *Sytsma et al. 4369* (CR, MO); ca. 800 m, *Croat 25434* (F, MO); *Gentry & Dwyer 3683* (MO); 900–930 m, *Croat 37481* (F, MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76740* (MO, US); Cerro Gaital, 800–900 m, 8°37′N, 80°07′W, *McPherson 11211* (L, MO); 830–900 m, 8°36′N, 80°07′W, *Croat 74812* (MO, PMA); *Hartman 3962* (OS); 1000–1100 m, 8°37′N, 80°07′W, *McPherson 12150* (MO); N slope of Cerro Gaital, 800 m, 8°38′N, 80°07′W, *Churchill 3924* (F, MO). **Veraguas**: Santa Fe region, Alto de Piedra, 800–950 m, 8°33′N, 81°08′W, *Croat 67004* (MO); Parque Nacional Cerro Tute, Alto Piedra–Calovébora, 0.5 mi. N of Alto Piedra, 800–1030 m, *Croat & Zhu 76897* (MO); 1000–1250 m, *Croat 48931* (MO).

Philodendron ligulatum Schott, Prod. Syst. Aroid. 224. 1860. TYPE: Cultivated from Central America, *Wendland s.n.* (holotype, W? destroyed). Costa Rica. Limón: Ref. Nac. Barra del Colorado, between Río Chirripocito and Río Sardina (Sardinal), 10°38′N, 83°45′W, 12 m, 22 Apr. 1990, *Grayum 9823* (neotype, MO; isoneotype, CR). Figures 269–271.

Hemiepiphytic, usually scandent or appressed-climbing or sometimes epiphytic, sometimes occurring high into canopy, rarely terrestrial; stem appressed-climbing or scandent (flowering stems often loose, semi-erect or spreading), green, sometimes with white, waxy coating; leaf scars conspicuous, 1.5–2 cm long, 1–1.8(3) cm wide; internodes sometimes weakly flattened on one side, (1)3–9(20) cm long, 0.5–3 cm diam., usually longer than broad, medium to dark green or gray-green to brownish, weakly glossy, drying gray-green to pale yellow-brown, sometimes irregularly ridged or cracked, sometimes closely tranverse-fissured; epidermis peeling, bubbling or with loose flakes; roots several per node, 15–45 cm long, drying 1–2 mm diam.; cataphylls usually sharply 2-ribbed, sometimes weakly and bluntly 1–2-ribbed, sometimes sharply D-shaped with adaxial margins winged to 6 mm high, 14–19 cm long, sharply flattened, with obtuse medial rib, green to whitish, sometimes tinged reddish, densely dark-lineate, sometimes densely dark-speckled, deciduous intact, margins minutely undulate; **petioles** (7)20–38 cm long, 5–15 mm diam., subterete to obtusely flattened, rarely D-shaped, sometimes with a thin, medial rib toward apex, sometimes with adaxial margins winged to 6 mm high, spongy but brittle (fresh), medium to dark green, obtusely to sharply flattened to sulcate adaxially, the margins at least sometimes acute, broadly rounded abaxially, surface matte to semiglossy, densely short dark green-lineate or speckled, with a deep maroon to purple ring around apex; sheath flattened, unopened, to 3–10 cm long, for up to half the length of the petiole; **blades** oblong-elliptic to narrowly ovate or narrowly oblanceolate-elliptic, subcoriaceous, weakly to moderately bicolorous, acuminate to long-acuminate at apex (the acumen inrolled or apiculate and sometimes downturned, 1–4 mm long), subcordate, obtuse to narrowly rounded or weakly cordate at base, (14)18–61 cm long, 8–19 cm wide (1.57–5.4 times longer than wide), (1.1–3.89(6.3) times longer than petiole), margins weakly undulate; upper surface dark green, semiglossy to moderately glossy, drying blackish brown to dark grayish or grayish brown, lower surface moderately paler, matte to weakly glossy, mottled violet-purple or maroon, drying dark olive-green to yellow-brown, dark olive-brown or dark brownish black; posterior lobes, when present, rounded to narrowly rounded, about as broad as long, 4–5 cm long, 5.5–6.6 cm wide, held close to petiole; sinus somewhat V-shaped, 0.5–3 cm (mostly 2.5 cm) deep; midrib flat to broadly convex, concolorous to paler than surface, sometimes sparsely purple-speckled near base above, narrowly rounded to convex to broadly convex, sometimes round-raised, paler or darker than surface, or sometimes concolorous below, sometimes sparsely purple-speckled near base below; basal veins not evident or 1–3 per side; primary lateral veins 4–8(12) per

side, departing midrib at a 40–70(75)° angle, ± straight or slightly curved to the margins, dark green, weakly sunken to etched, concolorous above, weakly raised to convex and paler than surface below (sometimes with purple spots on older leaves), drying brownish; interprimary veins obscure to impressed, paler than surface, weakly sunken above, weakly raised, darker than surface below; minor veins weakly visible above, very close, obscurely and weakly raised, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 1(2) per axil; peduncle (5)7.5–17.5(28) cm long, 7–10 mm diam., subterete, obtusely angular to 3-sided, pale to medium green; **spathe** 10–19.5 cm long, 1.5–2 cm diam. (to 6.5 cm wide when flattened), ((0.8–1.3)1.4–1.6(1.8) times shorter than peduncle), semiglossy, acuminate at apex, barely or not at all constricted, ribbed on back, margins revolute; spathe blade white or cream, sometimes sparsely red-spotted outside, sometimes tinged purple-violet on outer margin, 7–8.5 cm long, 1.7 cm diam. (opening 7.5–7.8 cm long, 3.2–4 cm wide), whitish inside; resin canals bright orange, appearing throughout lower ¾ of spathe and to near base of tube inside; spathe tube oblong, pale to medium green with pale violet nearest base, sparsely red-spotted outside, 6.5–7 cm long, 1.2–1.5 cm diam., glossy, whitish or pale green, sometimes red to violet-purple (B & K purple 5/10) near base or throughout tube inside; **spadix** ± tapered with slight bend, held ± erect, protruding forward from spathe, rounded at apex, (8.3)11–15.5 cm long; pistillate portion light green, (1.4)3.7–6.5 cm long, 9–13(16) mm diam. at apex, 10–14(17) mm diam. at middle, 9–12(15) mm diam. at base; staminate portion (6.8–7.2)10.5–11.2 cm long; fertile staminate portion (9)11–16 mm diam. at base, (7)11–16 mm diam. at middle, (5)9–11 mm diam. ca. 1 cm from apex, broadest slightly above the middle, as broad as or broader than the pistillate portion, as broad as or slightly narrower than the sterile portion; sterile staminate portion generally broader than pistillate portion, whitish or tinged faintly violet, 1–1.2 cm diam.; pistils 1.2–2.7(3.5) mm long, (0.8)1.1–1.9(2.6) mm diam.; ovary (5)6–8-locular, 0.8–1.8(2.4) mm long, (0.8)1.1–1.9(2.6) mm diam., walls embedded with granular, crystal-like particles; locules (0.8)1.1–1.8(2.4) mm long, (0.1–0.2)0.4–0.7 mm diam., ovule sac 0.5–0.7(1–1.3) mm long, with sub-basal placentation; ovules 1 per locule, contained within translucent, gelatinous envelope, 0.2–0.6 mm long, usually longer than funicle; funicle 0.1–0.2(0.4) mm long, style 1–6 mm long, (0.8–10)14–19(26) mm diam., similar to style type B or type D (rarely to type C); central style dome sometimes present; style apex flat to rounded or sloping; style boss sometimes present; funnel shallow when present; stigma somewhat cupulate, truncate, unlobed to subdiscoid, (0.4)0.9–12 mm diam., 0.1–0.3 mm high, covering center of or entire style apex, inserted on center of style apex or style boss or funnel if present, sessile, papillate, semiglossy; the androecium truncate, margins irregularly 4–6-sided, 1–3 mm long; thecae oblong to ovate, sometimes elliptical, 0.3–0.6 mm wide, ± parallel to one another or contiguous; pollen subspheroidal to oblong or obovoid; sterile staminate flowers usually 4–6-sided, 1.2–2.2 mm long, 1.3–2 mm wide. INFRUCTESCENCE with berries oblong-elliptic, 3 mm long; seeds oblong, light yellow-brown, 1.4 mm long, 0.4 mm diam., narrowly ribbed longitudinally. JUVENILE blades with lower surface sometimes tinged maroon.

Philodendron ligulatum ranges from Nicaragua (Chontales and Zelaya) along the Atlantic slope of Costa Rica and along the Atlantic slope and Continental Divide of Panama to Colombia (Antioquia and Chocó). It occurs in *Tropical wet forest* and *Premontane rain forest* life zones, from sea level to 1200 m elevation (to 600 m in Nicaragua and 650 m in Costa Rica).

Philodendron ligulatum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is characterized by its somewhat scandent to appressed-climbing habit; generally elongate internodes; sharply 2-ribbed to obtusely 1-ribbed cataphylls; more or less spongy, obtusely flattened to somewhat D-shaped petioles clearly demarcated from the blade by a purple ring; usually more or less oblong blades narrowly cordulate at the base (or with the blades ovate and cordate) with usually 1–2 free basal veins; and usually 1–2 inflorescences per axil.

This species comprises three varieties. *Philodendron ligulatum* var. *ligulatum* exists throughout the range of the species, whereas varieties *ovatum* and *heraclioanum* are endemic to Panama. See under those varieties for the differences separating them from variety *ligulatum. Philodendron ligulatum* var. *ovatum* is endemic to central Panama in Coclé and Veraguas Provinces, while *P. ligulatum* var. *heraclioanum* is known from far eastern Panama in San Blas and Darién.

Philodendron ligulatum is probably close to *P. correae* from upland Chiriquí in western Panama. The latter species differs in lacking distinct primary lateral veins. It also differs in occurring at generally higher elevations (780–1400 m).

Philodendron ligulatum may also be confused with *P. immixtum*, also a vine but with smaller leaves. See under the latter species for a discussion of the differences. *Philodendron ligulatum* may also be confused with *P. wendlandii*. The latter has similar blades and spongy petioles, but differs in being a true epiphyte with short internodes and petioles sharply flattened adaxially and usually much broader than thick.

The protologue of *P. ligulatum* describes a sterile plant, whereas Schott's color plates (Icones) depict fertile material. None can therefore be used as type material. In addition, Engler's *Araceae No. 180* prepared in 1883 and said to have been collected from the living type plant was not studied by Schott. This species is represented by excellent illustrations of fertile material by Schott, one of which could have served as a neotype, but it was deemed best to select a new fertile specimen for the neotype.

The names *Philodendron ligulatum* and *P. lingulatum* (L.) K. Koch (*P.* subg. *Pteromischum*) have been confused in the past. Pursuant to an unpublished request for a recommendation by the Committee for Spermatophyta, the two names have officially been ruled not confusable, hence not homonymous (see Nicolson, 1994: 280).

KEY TO THE VARIETIES OF *P. LIGULATUM*

1a. Petioles sharply D-shaped with undulate lateral margins adaxially; lower leaf blade surface mottled purple-violet or maroon; ovaries with 2 ovules per locule (lacking an obvious ovule sac); eastern Panama, 0–200 m var. *heraclioanum* Croat

1b. Petioles subterete, at most obtusely somewhat flattened adaxially; lower leaf blade surface not colored; ovaries with 1 ovule per locule, contained within an obvious ovule sac; Nicaragua to Panama.

2a. Leaf blades 1.5–1.7 times longer than wide; peduncles longer than spathe; Panama, 770–1200 m ..... var. *ovatum* Croat

2b. Leaf blades 2–4.5 times longer than wide; peduncles shorter than or about as long as spathe; usually occurring below 800 m (rarely to 1200 m) ..... var. *ligulatum*

Philodendron ligulatum Schott var. **ligulatum**

Internodes sometimes weakly flattened on one side, (1)3–9(2) cm long, 0.5–3 cm diam.; cataphylls usually sharply 2-ribbed, sometimes weakly 2-ribbed; **petioles** 7–38 cm long, 5–15 cm diam., subterete, usually at most obtusely somewhat flattened adaxially, sometimes sulcate, sometimes sharply flattened on one margin adaxially, rarely D-shaped; lower leaf blade surface not colored; blades oblong-elliptic, 24–60 cm long, 8–19 cm wide (2.1–4.4 times longer than wide), (1.1–3.9(5.1) times longer than petiole), upper surface drying dark olive-green to brownish; sinus 0.5–3 cm (mostly 2.5 cm) deep; basal veins not evident or 1–3 per side; primary lateral veins 5–8(9) per side, departing midrib at 60–70° angle. INFLORESCENCES 1 per axil; peduncle 7.5–17(28) cm long; **spathe** 10–19.5 cm long, spathe blade white or cream, sometimes sparsely red-dotted outside, spathe blade whitish or sometimes violet-purple near base of tube or throughout inside; spathe tube pale green thoughout, pale violet nearest base, sometimes sparsely red-violet outside; **spadix** (8.3)11–15.5 cm long; pistillate portion (1.4)3.7–6.5 cm long; ovules 1 per locule, contained within an obvious ovule sac; style similar to style type B or D, central dome sometimes present; stigma somewhat cupulate, truncate, unlobed to subdiscoid.

Flowering in *Philodendron ligulatum* var. *ligulatum* occurs in the early rainy season, between May and August, with a few flowering collections from October through March at the end of the rainy season and early dry season. Post-anthesis inflorescences have been collected from February through August (as well as November). It is possible that this species flowers bimodally, once near the beginning of the rainy season and again near the end of the rainy season or the early dry season. Immature fruits are known from July, August, and December, but mature fruits only from December.

Philodendron ligulatum is typically somewhat scandent in Costa Rica but is often more nearly an appressed hemiepiphyte in Panama. In Costa Rica, the number of inflorescences per axil is never more than two but in some areas of Panama up to three inflorescences per axil may be encountered, and in the Santa Rita Ridge area of Panama, a particularly unusual specimen (*Croat 76954*) has up to five inflorescences per axil. That collection also has proportionately somewhat longer petioles than other collections. This unusual specimen is otherwise identical to other plants of the species, even those from the same region. It is perhaps of hybrid origin.

A few Panamanian specimens of *P. ligulatum* var. *ligulatum* from the vicinity of Santa Fe in Veraguas Province (*Croat 25692, 48906A, 66914*) and in Coclé (*Croat 49195*) differ in drying yellow-green and having somewhat more coarse venation. These are somewhat intermediate with *P. ligulatum* var. *ovatum*.

Croat 33306, from 1200 m elevation on Cerro Colorado in eastern Chiriquí Province, has black-drying blades averaging slightly more than two

times longer than broad, and is also somewhat intermediate with *P. ligulatum* var. *ovatum*.

A collection from the southern slopes of Panamá Province in the basin of the Río Madroño (*Croat & Zhu 77041*) is intermediate between *P. ligulatum* var. *heraclioanum* and variety *ligulatum* in having sharply D-shaped petioles lacking undulate-winged margins.

A noteworthy collection from Antioquia Department in Colombia (*Fonnegra et al. 1957*) perhaps also represents *P. ligulatum* var. *ligulatum*, but differs in having the primary lateral veins drying paler than the surface below rather than darker as is the general case.

Additional specimens examined for P. ligulatum *var.* ligulatum. COSTA RICA. **Alajuela**: 3 mi. N of San Miguel, 380 m, *Croat 35643* (MO); Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36262* (MO); near Río Zapote, 1.8–2.7 km S of Río Canalete, ca. 100 m, *Croat 36360* (MO); Naranjo–Aguas Zarcas, 8.5 km NE of Villa Quesada, ca. 600 m, *Croat 46971* (MO). **Guanacaste**: Parque Nacional Rincón de la Vieja Colecta, 400 m, *Rivera 1136* (CR, MO). **Heredia**: La Zona Protectora, SSE of Magsasay, *Schatz & Grayum 707* (DUKE); Finca La Selva, at confluence of Río Sarapiquí and Río Puerto Viejo, Atlantic slope, 50–80 m, 10°26′N, 84°01′W, *Grayum 7673* (CR, MO); *Folsom 9973* (MO); 100 m, *Grayum 2800* (MO); *Hammel 8827* (MO); *Croat 61220* (MO); between Río Sucio and railroad tracks, SW of Finca Zona Ocho, Río Frío de Sarapiquí, ca. 110 m, 10°18′N, 83°52′30″W, *Grayum & Hammel 5567* (CR, MO); near Porto Viejo along road near Río Sucio, 20 m, *Croat 35730* (MO). **Limón**: Hitoy Cerere reserve, SW of Valle La Estrella, 150–550 m, 9°39′N, 83°02′W, *Grayum et al. 5806* (CAS, CR, MO, PMA, US); Turrialba–Limón, ca. 11 mi. S of Siquirres, 650 m, *Croat 43331* (MO); Refugio Nacional de Vida Silvestre Barra del Colorado, Río Chirripocito–Río Sardina, 12 m, 10°38′N, 83°45′W, *Grayum 9823* (CR, MO). NICARAGUA. **Chontales**: Cerro Las Nubes, El Tamagás–Loma San Gregorio, ca. 2 km N of Santo Domingo, 600 m, *Grijalva & Ríos 3455* (MO). **Matagalpa**: NW of Cerro Musún, 500–800 m, *Araquistain & Moreno 2570* (MO). **Zelaya**: Colonia Kururia, <50 m, ca. 14°41′N, 84°04′W, *Pipoly 3974* (MO); plantel of Neptune Mining Company, NE Bonanza, 200–350 m, ca. 14°01′N, 84°35′W, *Stevens 13029* (MO); Río Iyas, between Quebrada El Toro, 260–280 m, *Vincelli 371* (MO); Río Sucío, 2 km E of Bonanza, 140 m, *Neill 4011* (K, MO). PANAMA. **Bocas del Toro**: Station Milla 7.5 on Changuinola–Almirante Railroad, 100 m, *Croat 38098* (CM, COL, CR, F, MO, NY); Almirante–Ojo del Agua, 3–6 km W of Almirante, 30–200 m, *Croat 38212* (F, K, MO); vic. of Chiriquí Lagoon, *Wedel 1479* (F, GH, MO). **Canal Area**: along Río Indio de Gatún, near sea level, *Pittier 2794* (US). **Chiriquí**: Cerro Colorado, along Continental Divide 20–28 mi. from San Félix, 1200–1500 m, *Croat 33306* (MO). **Coclé**: La Mesa, N of El Valle de Antón, 785 m, 8°37′N, 80°08′W, *Croat 67113* (MO, PMA); 800 m, *25370* (F, MO, US); 800 m, 8°36′N, 80°07′W, *Croat & Zhu 76669* (MO); *76694* (CM, MO, NY, PMA); Alto Calvario, 5.2 mi. above El Copé, 930 m, *Croat 49195* (BR, CM, DUKE, F, GH, HNMN, MO, PMA, TEX, WIS); 750–900 m, *44734* (MO); 2700 ft., *Sytsma et al. 4343* (MO); Quebrada Mollejón, ca. 5 mi. N of El Copé, 700 m, *Croat 75050* (MO); road to Coclesito, 12 mi. from Llano Grande, 200 m, 8°47′N, 80°28′W, *Churchill et al. 4018* (F, MO). **Colón**: Santa Rita Ridge road, ca. 22 km from Transisthmian Highway, 500 m, 9°25′N, 79°40′W, *Hammel et al. 14474* (L, MO); along trail to Río Indio, beginning 10.6 km from highway, 380 m, *Croat 34302* (MO, NY, PMA); 26 km from highway, 500 m, 9°26′N, 79°57′W, *Knapp et al. 1737* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76954* (B, CAS, COL, CR, F, K, MEXU, MO, NY, PMA, SCZ, US, VEN); Sabanitas–Portobelo, Río Piedras Lumber Road, 250 m, 9°22′30″N, 79°41′30″W, 250 m, *Croat 75164* (MO, PMA); *75171* (MO); Portobelo–Nombre de Dios, 4.1 mi. W of Nombre de Dios, 50 m, 9°35′N, 79°33′W, *Croat 67318* (AAU, CAS, CM, COL, CR, DUKE, F, G, HNMN, K, KYO, L, LE, MBM, MO, NY, P, PMA, QCA, RSA, TEX, US, VDB); Portobelo–Nombre de Dios, vic. Río Indio, 50 m, *Croat 33603* (MO, PMA); above road 18 km past Sardinilla on road to Nombre de Dios, 150–300 km, *Croat 26100* (MO); Río Boquerón, past Salamanca, 300–400 m, 9°20′N, 79°35′W, *Knapp & Sytsma 2389* (MO); Río San Augustín flowing into Río Guanche, ca. 0 m, 9°30′N, 79°40′W, *Churchill et al. 6017* (CAS, MO, NY, PMA, RSA); Río Iguanita–Portobello Road, <50 m, 9°27′N, 79°42′W, *Croat 49778* (F, MO); Río Guanche above bridge on Portobelo Road, ca. 3–5 km above bridge, 50–200 m, *Croat 36970* (MO); 4 km up Río Guanche, 0–50 m, 9°30′N, 79°40′W, *Knapp 997* (MO); ca. 1.5 mi. S of road, <100 m, 9°27′N, 79°40′W, *Croat & Zhu 76237* (MO); vic. of Guásimo on Río Miguel de la Borda, *Knapp 9983* (MO, SCZ); Río Fató, 10–100 m, *Pittier 3867* (NY, US). **Panamá**: El Llano–Cartí Road, 6.8 mi. from highway, 350 m, *Croat 49102* (MO); Cerro Jefe, 15.4 mi. from Panamerican Highway, ca. 1000 m, *Croat 49092* (MO); Serranía de Majé, high point of ridges S of Ipetí, 650–800 m, 8°45′N, 77°30′W, *Knapp et al. 4490* (MO); El Valle de Madroño–La Saena, 2.5 mi. N of El Valle de Madroño, 180 m, 9°14′25″N, 79°05′W, *Croat & Zhu 77041* (MO). **San Blas**: El Llano–Cartí Road, 1–2 mi. N of Nusagandi on road to Cartí, 250–275 m, 9°20′N, 79°W, *Croat & Zhu 76580A* (MO). **Veraguas**: vic. of Sante Fe, past Escuela Agrícola Alto de Piedra, at Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66914* (MO, US); ca. 5–8 km beyond agricultural school, 730–770 m, *Croat 25962* (F, MO); Santa Fe–Calovébora, 1.7 mi. past Alto Piedra School, 1.5 mi. beyond Quebrada Cosilla, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76862* (MO); Río Concepción, *Lewis 2793* (MO, NY).

Philodendron ligulatum var. **heraclioanum** Croat, var. nov. TYPE: Panama. Darién: Parque Nacional Cerro Pirre, vicinity of station along Río Perisenico, 110 m, 8°01′N, 77°44′W, 26 July 1994, *Croat & Zhu 77098* (holotype, MO– 04619347–9; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, GB, GH, HUA, IBE, K, L, M, MEXU, NY, OOM, P, PMA, QCA, SEL, TEX, U, US, VEN, WIS). Figures 274–276.

Internodia 1 cm longa, 1.1–2.5 cm diam.; cataphylla 15–20 cm longa, obtuse 2-costata, decidua; petiolus acute D-formatus, (8.5)20–28 cm longus, marginibus alatis; lamina (29)46–61 cm longa, (8.5)12–15 cm lata, oblongo-elliptica vel anguste oblanceolato-elliptica, obtusa basi, in

sicco nigrescens; inflorescentia 1; pedunculus (5)13–15 cm longus, 1 cm diam.; spatha 10–12 cm longa.

Internodes short, to 1 cm long, 1.1–2.5 cm diam., usually longer than broad, medium green, semi-glossy, drying pale yellow-brown, conspicuously and irregularly ridged and cracked; roots moderately few, to 30 cm long, 4 mm diam., reddish brown, weakly glossy, finely scaly; cataphylls 15–20 cm long, bluntly 1–2-ribbed, sharply 2-ribbed near apex; **petioles** (8.5)20–28 cm long, sharply D-shaped, with adaxial margins winged (to 6 mm high); **blades** oblong-elliptic to narrowly oblanceolate-elliptic, obtuse to narrowly rounded at base, (29)46–61 cm long, (8.5)12–15 cm wide ((2.9)4.3–5.4 times longer than wide), (2–2.6(6.3) times longer than petiole), upper drying blackish, lower surface matte, heavily tinged or mottled violet-purple or maroon, drying dark brownish black; midrib narrowly rounded and paler than surface below with maroon spots on older veins; basal veins lacking; primary lateral veins 5–12 per side, departing midrib at a 40–50° angle to the margins, green with maroon spots on older plants. INFLORESCENCES 1 per axil; peduncle (5)13–15 cm long, 1 cm diam.; **spathe** pale green, 10–12 cm long, to 6.5 cm wide when flattened, tinged violet-purple on outer margin and at base outside and at base inside; spathe blade greenish inside; spathe tube pale green, glossy inside; **spadix** 9.5–12 cm long; pistillate portion 4.3 cm long in front, 3.6 cm long in back; ovules 2 per locule, contained within transparent matrix, style similar to style type C; style funnel shallow to moderately deep. INFRUCTESCENCE with berries oblong-elliptic, 3 mm long; seeds oblong, light yellow-brown, 1.4 mm long, 0.4 mm diam., narrowly ribbed longitudinally. JUVENILE blades with lower surface heavily tinged maroon.

Flowering in *Philodendron ligulatum* var. *heraclioanum* is poorly known. Pre-anthesis flowering collections were seen from March and in July. The inflorescence on the July collection was nearly fully emerged so that it would certainly have opened in less than one month. Immature fruits were seen in October.

Philodendron ligulatum var. *heraclioanum* is endemic to Panama, known definitely only from the type locality at the base of Cerro Pirre in Darién Province from 50 to 200 m elevation in a *Premontane wet forest* life zone.

This variety is characterized by its bluntly two-ribbed cataphylls; sharply D-shaped, marginally winged petioles; and the oblong-elliptic to narrowly oblanceolate-elliptic, blackish drying blades heavily tinged with maroon on the lower surface when young.

Philodendron ligulatum var. *heraclioanum* differs from both varieties *ligulatum* and *ovatum* in its sharply D-shaped petioles with undulate-winged margins; in having 2 ovules per locule without an obvious ovule sac (vs. 1 ovule per locule contained in an ovule sac for the other two varieties); and in the maroon coloration of the lower surface of the young blades. In contrast, the other two varieties have petioles that are typically terete or subterete, merely obtusely flattened adaxially.

Philodendron ligulatum var. *heraclioanum* may be confused with *P. pseudauriculatum*, but the latter differs in having the petioles unwinged and, at most, obtusely flattened adaxially. In addition, *P. pseudauriculatum* has never been reported to have the blades purplish on the lower surfaces.

A collection from San Blas in far eastern Panama is probably also this variety; it differs in having much longer internodes (to 10 cm long and drying ca. 5 mm diam.) and proportionately shorter petioles.

Philodendron ligulatum var. *heraclioanum* is named in honor of Panamanian collector Heraclio Herrera, who was one of the first to collect the taxon.

Additional specimens examined. PANAMA. **Darién**: Cerro Pirre National Park, W side of Cerro Pirre, base camp, 50 m, 8°N, 77°48′W, *Croat 68963* (MO); Parque Nacional Darién, Estación Rancho Frío, N base of Cerro Pirre, ca. 9 km S of El Real, Quebrada Perisenico, 70–270 m, 8°01′N, 77°44′W, *Hammel et al. 16145* (MO). **San Blas**: Quebrada Masargandí, Isla de Tubuala, 200–400 m, 8°54′N, 77°46′W, *Herrera 1304* (CAS, CM, MO, PMA).

Philodendron ligulatum var. **ovatum** Croat, var. nov. TYPE: Panama. Veraguas: vicinity of Santa Fe, along road between Alto Piedra and Calovébora, 0.5 mi. N of Alto Piedra, on slopes of Cerro Tute, Parque Nacional Cerro Tute, 800–1030 m, 15 July 1994, *Croat & Zhu 76888* (holotype, MO– 4619517; isotypes, B, COL, CR, F, K, NY, PMA, US, VEN). Figure 273.

Internodia 1–6(8) cm longa, 1–1.7(3) cm diam.; cataphylla 13–16 cm longa, incostata vel acute 2-costata; petiolus (10)15–19 cm longus, 7 mm diam.; lamina anguste ovata, subcordata basi, (14)18–26(39) cm longa, (8.5)12.5–16 cm lata, in sicco viridibrunnea supra, flavibrunnea infra; inflorescentia 1; pedunculus 12–16.5 cm longus, 7–10 mm diam.; spatha 11.5–18.5 cm longa, extus omnino viridalba; tubo spathae intus rubro basi.

Internodes 1–6(8) cm long, 1–1.7(3) cm diam., sometimes to 3 m or more long, sometimes covered with a thin layer of translucent white wax; cata-

phylls 13–16 cm long, unribbed to bluntly 1-ribbed or sharply 2-ribbed (ribs to ca. 4 mm high, incurled); **petioles** (10)15–19 cm long, 7 mm diam., subterete and obtusely flattened toward apex; **blades** narrowly ovate, weakly cordate at base, (14)18–26(39) cm long, (8.5)12.5–16 cm wide (1.57–1.65 times longer than wide), upper surface drying greenish brown to blackened, lower surface drying yellowish brown to dark olive-brown; posterior lobes rounded to narrowly rounded, 4–5 cm long, 5.5–6.6 cm wide, narrowly rounded to obtuse; sinus somewhat V-shaped, 2.5–3 cm deep; midrib convex to round-raised below; basal veins 2–3 per side, free to base; primary lateral veins 4–6 per side, departing midrib at a 55–65(75°) angle. INFLORESCENCES 1 per axil; peduncle 12–16.5 cm long, 7–10 mm diam.; **spathe** 11.5–18.5 cm long, 1.5–2 cm diam. (0.8–0.95 times as long as peduncle), greenish white throughout; spathe tube sometimes pale to medium green outside, pale to medium green, sometimes red to purplish violet at base inside; **spadix** 10–12.5 cm long; pistillate portion 4–4.5 cm long; pistils 1.7–1.8 mm long, 1.7–1.8 mm diam., whitish; ovules 1 per locule, contained within transparent, gelatinous ovule sac, style similar to style type B; stigma subdiscoid, unlobed, often truncate.

Flowering in *Philodendron ligulatum* var. *ovatum* occurs in the rainy season. Collections at or near anthesis have been made in July, October, and November. Observations on a single plant in July showed a series of inflorescences with one at anthesis and one other on the same stem in postanthesis condition. No fruiting collections are known.

Philodendron ligulatum var. *ovatum* is endemic to Panama, known only from Santa Fe in Veraguas and at El Copé in Coclé Province in *Premontane rain forest* at 770 to 1200 m elevation.

This taxon is characterized by its smooth, brown-drying stems, elongate internodes, sharply 2-ribbed to bluntly 1-ribbed deciduous cataphylls, subterete to D-shaped petioles about as long as the blades, ovate, subcordate blades with two to three pairs of free basal veins, and solitary inflorescences with the peduncle longer than the spathe.

Philodendron ligulatum var. *ovatum* differs from variety *ligulatum* in having blades 1.5–1.7 times longer than wide (vs. 2–4.5 times longer than wide in var. *ligulatum*); peduncles longer than the spathe (vs. shorter than or about as long as the spathe for var. *ligulatum*); and two ovules (rather than one) per locule. In addition, *P. ligulatum* var. *ovatum* usually occurs at higher elevations (770 to 1200 m) vs. usually below 800 m for *P. ligulatum* var. *ligulatum*. Curiously, leaves of a few specimens of *P. ligulatum* var. *ovatum* dry yellowish green or brown, as opposed to the somewhat blackened color typically associated with the species.

Philodendron ligulatum var. *ovatum* may also be confused with *P. lentii* Croat & Grayum with which it also occurs in the El Copé region. That species differs in having usually more than ten pairs of primary lateral veins with several pairs of interprimary veins visible between them on the dried upper blade surfaces (vs. only about five pairs of primary lateral veins and no interprimaries visible on the upper dried blade surface). In addition, the spathes of *P. lentii* are typically short-pedunculate.

Additional specimens examined. PANAMA. **Coclé**: Alto Calvario, ca. 6 mi. N of El Copé, 770 m, 8°38′N, 80°35′W, *Croat & Zhu 76754* (MO); *Croat 67572* (MO); *68767A* (CM, MO); 1200–1300 m, 8°38′N, 80°36′W, *Sytsma 1903* (MO); 650–850 m, *Folsom 6221* (MO, PMA); ca. 5 mi. N of El Copé, 900–1000 m, *Croat & Zhu 75055* (K, MO, SCZ). **Veraguas**: vic. Escuela Agrícola Alto Piedra near Santa Fe, 1050–1150 m, *Croat 48906A* (MO).

Philodendron llanense Croat, sp. nov. TYPE: Panama. Panamá: vic. of Cerro Jefe, along road to summit which leads S off main road to La Eneida, 750–800 m, 9°14′N, 79°22′W, *Croat 67092* (holotype, MO–3582669–71; isotypes, B, CAS, COL, CR, F, G, HUA, K, M, MEXU, NY, P, PMA, SCZ, SEL, TEX, US, VEN). Figures 268, 277, 278.

Planta plerumque hemiepiphytica, raro terrestris; internodia 5–10 cm longa, 4–6 cm diam.; cataphylla 30–41 cm longa, plerumque incostata, persistentia semi-intacta aut ut fibrae nodis supremis; petiolus subteres, 49–76 cm longus, 1–2 cm diam.; lamina 51–77 cm longa, 39–60.4 cm lata, late ovato-cordata; nerviis lateralibus I (4)5–6(7) utroque; inflorescentia (1)2–3; pedunculus 3–10.5 cm longus; spatha 12.5–24 cm longa, lamina spathae extus atriviridi, intus alba; tubo spathae atrirubroviolaceo basi; pistilla (5)6–8(9)-locularia; loculi (6)12(20)-ovulati.

Usually hemiepiphytic, rarely terrestrial; stem appressed-climbing, to 1 m long, sap clear, viscous, sticky, spicy- to turpentine-like-scented; internodes usually short, dark green, soon gray-green, finally light brown, moderately scurfy, semiglossy, 5–10 cm long, 4–6 cm diam., usually broader than long, sometimes longer than broad; roots greenish, becoming brown, 3–4 mm diam.; cataphylls 30–41 cm long, usually unribbed, sometimes weakly 2-ribbed, light to medium green, sharply and broadly D-shaped, persisting semi-intact or as fibers at uppermost nodes, fibrous below, the fibers thin, pale, disorganized, light gray. LEAVES erect-spreading, clustered at or near stem apex; **petioles** 49–76 cm

long, 1–2 cm diam., subterete, somewhat spongy, pale to medium green, rarely with medial rib adaxially, with adaxial margins sometimes acute, surface semiglossy to almost matte, densely and in conspicuously short-lineate, at least sometimes with a dark green ring at apex; **blades** broadly ovate-cordate, moderately coriaceous, abruptly acuminate, sometimes acute at apex, conspicuously cordate at base, 51–77 cm long, 39–60.4 cm wide (1.2–1.6 times longer than wide), (0.9–1.2 times longer than petiole), about equal in length to petiole, margins ± hyaline, upper surface dark green, semiglossy to moderately glossy, drying dark brown, lower surface semiglossy to almost matte, paler, drying yellow-brown; anterior lobe 41–60 cm long, 39–60.4 cm wide (0.9–1.4 times longer than wide), (2.2–3 times longer than posterior lobes); posterior lobes 18.5–24 cm long, 16–31 cm wide, obtuse; midrib almost flat to broadly convex to broadly flattened, paler than surface above, convex, paler than surface below; basal veins 4–6 per side, with 0–1 free to base, the remaining coalesced 6–9 cm; posterior rib usually naked for 2–3 cm; primary lateral veins (4)5–6(7) per side, flat to weakly sunken, paler than surface above, convex, paler than surface below; minor veins moderately obscure above, darker than surface, arising from both the midrib and primary lateral veins, drying prominulous above and below; secretory canals distinct. INFLORESCENCES (1)2–3 per axil; peduncle 3–10.5 cm long, 1.1–1.2 cm diam., coarsely white striate near apex; **spathe** 12.5–24 cm long (1.7–5 times longer than peduncle), oblong, dark to medium green throughout outside, markedly white-lineate near the base, faintly so above the base, moderately constricted above the tube; spathe blade weakly and densely lineate outside (opening broadly elliptic in face view), white inside; spathe tube cylindrical, markedly white-lineate near the base outside, 6–8.5 cm long, 3–5.5 cm diam., dark reddish violet, suffused onto base of blade inside; **spadix** sessile, greenish white throughout, ± cylindrical, protruding prominently forward from and out of the end of spathe (at anthesis), 10–17 cm long; pistillate portion creamy white (anthesis), reddish (pre-anthesis), weakly tapered toward apex, 4.1–5 cm long, 2.5–5 cm long in front, 1 cm diam. throughout, 1.1–1.5 cm diam. at apex, 1.4–1.6 cm diam. at middle, 1–1.5 cm wide at base; staminate portion 6–14.4 cm long; fertile staminate portion white, ± cylindrical 1.1–1.7 cm diam. at base, 1.1–1.9 cm diam. at middle, 7–10 mm diam. ca. 1 cm from apex, broadest ± at the middle, slightly broader than the pistillate portion, narrower than the sterile portion; sterile staminate portion 1.1–1.9 mm diam.; pistils 1.2–4.8(7.2) mm long, 1.1–2.4(4.3) mm diam.; ovary (5)6–8(9)-locular, 1.5–3.5(6.8) mm long, 1.1–2.4(4.3) mm diam., walls sometimes embedded with granular, crystal-like particles, locules 1.5–3.5(6.8) mm long, (0.2)0.6–1.5 mm diam., thin and membranous, ovule sac 1.9–2 mm long, with axile placentation; ovules (6)12(20) per locule, 1–2-seriate, contained within gelatinous ovule sac, 0.2–0.45 mm long, slightly longer than funicle; funicle 0.1–0.3 mm long, style 0.3–0.7 mm long, 1.3–1.6(2.5, 4.5) mm diam., similar to style type B; style crown truncate at apex with lobed depression; style apex rounded; stigma button-like, unlobed or weakly lobed, truncate, 1.1–2.2 mm diam., 0.5–1.0 mm high, covering entire style apex, sometimes depressed medially; the androecium truncate, margins irregularly 4–6-sided; thecae oblong to cylindrical, 0.4 mm wide, ± parallel to one another, ± contiguous; sterile staminate flowers acutely to bluntly 4–6-sided, 2.1–2.4 mm long, 1.1–2 mm wide. INFRUCTESCENCE with spathe green outside, orange-brown inside; berries white, 7.2–10 mm long, 3.6 mm diam.; seeds more than 10 per locule, pale yellow. JUVENILE plants terrestrial or epiphytic; internodes short, brown, weakly glossy; petioles 29.2 cm long, ± terete, moderately spongy; blades 28.6–37.7 cm long, 17–28 cm wide; midrib broadly convex above; minor veins distinct below.

Flowering in *Philodendron llanense* occurs at the beginning of the rainy season, in July. Post-anthesis collections exist from January through August, with immature fruits and mature fruits found only in the dry season and early rainy season, mostly January and March but also in June.

Philodendron llanense is endemic to Panama (though to be expected in adjacent Colombia), ranging from 250 to 800 (mostly below 500) m elevation in *Tropical wet forest* and *Premontane rain forest* life zones. This species appears restricted to the region of the Cerro Jefe and the El Llano–Cartí Road (hence the name "llanense").

Philodendron llanense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is characterized by its short, thick internodes; mostly unribbed, semi-intact, or fibrous cataphylls; obtusely flattened to D-shaped petioles (about as long as the blades); thick, broadly ovate-cordate blades with a deeply spathulate to closed sinus and with prominently raised minor veins upon drying; and two to three green inflorescences with the spathe tube dark reddish violet inside.

Philodendron llanense is perhaps most easily confused with *P. schottianum*, which occurs at

mostly higher elevations (generally 1000 to 1600 m) in Costa Rica, rarely to as low as 490 m or as high as 2200 m elevation. It differs from *P. llanense* in having sharply two-ribbed cataphylls persisting more intact and with a prominent yellow epidermis, and blades usually drying with the lower surface more yellowish with the secretory ducts more outstanding and usually with partial "cross-veins" between the minor veins. In addition, *P. schottianum* also has blades proportionately somewhat longer (averaging 1.65 times longer than broad vs. 1.4 times longer than broad for *P. llanense*) and spathes shorter and nearly elliptic with almost no constriction (vs. oblong and noticeably constricted above the tube for *P. llanense*).

Philodendron llanense looks superficially much like *P. ferrugineum* in live condition, and since they occur together, they can be confused. However, *P. ferrugineum* differs in having promptly deciduous cataphylls and somewhat more elongate blades, which dry conspicuously reddish brown.

A single sterile collection (*Croat & Grayum 60209*) from the Atlantic slope near the Continental Divide at 590 m elevation in Bocas del Toro Province may also belong to this species. In addition to being out of range, this collection has the major veins much darker than the surface below.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna–Chiriquí Grande, 4.3 km N of the Continental Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60209* (MO). **Panamá**: El Llano–Cartí Road, 10–12 km from El Llano, 400 m, *Maas & Dressler 1709* (U); Km 9.5 of Pan-American Highway, 200–300 m, 9°15′N, 79°W, *McPherson 10822* (B, MO); Km 12, 350 m, *Mori et al. 4628* (MO); Mile 7, 460 m, 9°19′N, 79°59′W, *Croat 75104* (CAS, MEXU, MO, NY); Km 8–12, ca. 400–450 m, *Nee et al. 8775* (MO, NY, SCZ); Mile 5–9, 200–250 m, 9°15–16′N, 78°59′W, *Thompson 4621* (CM); ca. Km 16–18, 400 m, *Tyson & Nee 7361* (MO, PMA, US); Mile 10.1, 325–350 m, *Croat 67367* (DUKE, K, M, MEXU, MO, NY, US); Mile 12, 200–500 m, *Croat 22910* (MO, PMA); Km 7–12, 360–400 m, *Croat 25118* (MO), *25172* (MO); Mile 10, 330 m, *Croat 33774* (MO), *33819* (MO); Mile 6.8, 350 m, *Croat 49127* (MO); Km 12, *Croat 26031* (MO); Cerro Jefe, near summit, <2900 ft., *Gentry et al. 3501* (MO, NY); 12 km E of Lago Azul, 800–1000 m, *Gentry & Mori 13450* (MO). **San Blas**: El Llano-Cartí Road, 300–500 m, *Liesner 1317* (F, MO, NY, US); Mile 14, 300 m, 9°15′N, 79°W, *Croat 69251* (F, MO); Mile 7, 550 m, 9°43′N, 78°68′W, *60505* (CM, MO, PMA); Km 22, 350 m, 9°19′N, 78°55′W, *de Nevers & Herrera 7859* (MO, PMA); Nusagandi, Sendero Wedar, 300–400 m, 9°18′N, 78°58′W, *McDonagh et al. 216* (BM, MO); 1–2 mi. N of Nusagandi on road to Cartí, 250–275 m, 9°20′N, 79°W, *Croat & Zhu 76577A* (CM, MO); Mile 10.1, 300 m, 9°20′N, 79°W, *76541* (MO, SEL); 1.9 mi. N of Nusagandi, 310 m, *76993* (AAU, CR, GB, MO, NY).

Philodendron madronense Croat, sp. nov. TYPE: Panama. Panamá: Valle de Madroño, ca. 10 road mi. N of La Margarita (near Chepo), just S of Continental Divide along main trail to Cangandí, 350–500 m, 9°19′N, 79°08′W, 21 Feb. 1986, *Hammel & McPherson 14526* (holotype, MO–3490432; isotypes, CM, M, PMA). Figures 279, 280.

Planta hemiepiphytica; internodia usque 2.5 cm diam., longiora quam lata; cataphylla decidua; petiolus subteres, usque 68 cm longus, 1.5 cm diam., aliquantum spongiosus; lamina trisectus, 39.5 cm longis, 15 cm latis; segmentis medianis ellipticis; segmentis lateralibus valde inequilateris, 32–32.8 cm longis, 12.7–13 cm latis; infructescentia 1. Inflorescentia 1; pedunculus usque 22 cm longus, 1 cm diam., in sicco denigratus; spatha usque 20 cm longa, ca. 4 cm diam.; spadix pistillata 11.8 cm longa, ca. 3 cm diam.; spadix staminata ca. 7.5 cm longa, ca. 1 cm diam.; 1 semen in quoque loculo.

Hemiepiphytic vine; internodes to 2.5 cm diam., longer than broad, epidermis drying light brown and semiglossy but conspicuously and irregularly folded; roots several per node, drying dark brown; cataphylls deciduous; **petioles** to 68 cm long, 1.5 cm diam., subterete, somewhat spongy, drying blackened, surface closely and finely ridged; sheathing to 8.5 cm long; **blades** trisect, subcoriaceous, moderately bicolorous, drying weakly glossy, upper surface dark green, drying dark brown, semiglossy, lower surface drying yellow-green, matte; median segments elliptic, somewhat inequilateral, 39.5 cm long, 15 cm wide (ca. 2.5 times longer than wide), (1.5 times longer than lateral lobes), somewhat acuminate at apex, base attenuate and somewhat inequilateral with leafy tissue extending to base on one side, ending 2.5 cm above the base of the other side; lateral segments markedly inequilateral, 32–32.8 cm long, 12.7–13 cm wide, acuminate; the outermost lobes with the inner margins attenuate, tissue ending 1–2.5 cm from base of petioles; outer margins rounded, barely or not at all naked along the sinus; midrib weakly raised, concolorous above, ± round-raised, drying blackened and irregularly ridged below; basal veins lacking; primary lateral veins ca. 25 per side, ca. 4–5 mm apart, departing midrib at a 65–70° angle toward apex, 85–100° angle toward base, gradually curved to the margins, weakly sunken, scarcely more conspicuous than interprimaries above, prominently raised below; interprimary veins numerous, 1–3 between each pair of primary lateral veins; minor veins in part undulate upon drying, close, moderately visible, arising from both the midrib and primary lateral veins. INFLORESCENCES (postanthesis) 1 per axil; peduncle to 22 cm long, 1 cm diam., drying blackened, somewhat spongy; **spathe**

to 20 cm long, ca. 4 cm diam., semiglossy, green outside, red at base inside, drying blackened; pistillate spadix 11.8 cm long, ca. 3 cm diam.; staminate spadix 7.5 cm long, ca. 1 cm diam., moderately tapered to a bluntly acute apex; pistils ± cylindrical, 3–4 mm long, 2.5 mm diam.; ovary 6–7-locular, with sub-basal placentation; locules 2.3 mm long, 0.5 mm diam.; ovules 1 per locule, contained within a transparent evelope; funicle ca. 0.4 mm long (can be pulled free to base), style similar to style type D; style apex flat; style boss pronounced but narrow; seeds 1 per locule, 1.4 mm long.

Flowering in *Philodendron madronense* apparently occurs in the rainy season, since immature fruits have been collected in January.

Philodendron madronense is endemic to central Panama along the border of Panamá and San Blas at 350 to 450 m elevation in a *Tropical wet forest* life zone.

Philodendron madronense is a member of *P.* sect. *Tritomophyllum*. This species is recognized by its scandent habit; elongate internodes; subterete, more or less spongy petioles; and especially by its trisect leaf blades with the medial segments elliptic, inequilaterally attenuate at the base, and with many close prominent primary lateral veins only 4–5 mm apart and departing the midrib at about a 90° angle.

Philodendron madronense is superficially most similar to *P. cotobrusense*, which has deeply 3-lobed blades with more or less elliptic, closely veined divisions. The latter species differs in having the lobes united and confluent at the base and up to five inflorescences per axil. It is also similar to some broad-leaved forms of *P. tripartitum* (e.g., *Whitefoord & Eddy 223*), which occur in eastern Panama, but those differ in having no more than 12 pairs of primary lateral veins, which depart the midrib at a 50–60° angle.

Philodendron malesevichiae Croat, sp. nov. TYPE: Panama. Coclé: vicinity El Valle de Antón, La Mesa, 4 mi. E of El Valle at base of Cerro Gaital, along trail which goes to the S edge and leading to the summit, 830–900 m, 8°36′N, 80°07′W, 25 Mar. 1993, *Croat 74818* (holotype, MO–4342656–57; isotypes, B, COL, CR, F, K, MEXU, NY, PMA, QCNE, US, VEN). Figures 3, 21, 25, 27, 28, 281–284.

Planta terrestris; caulis repens; internodia 2–4 cm longa, 1.5–5 cm diam.; cataphylla 21–29 cm longa, leniter 1–2-costata, in sicco rubrobrunnea, persistentia semi-intacta; petiolus teres, 50–56 cm longus, 8–19 mm diam., anguste sulcatus, sparsim squamus in triente superiore; lamina ovato-cordata, 33–65 cm longa, 23–36 cm lata, in sicco atribrunnea supra, flavibrunnea infra, nervis basalibus 6–9 paribus, superioribus 2–3 liberis ad aliquot basim; reliquiarum coalitis 2–4.5 cm; inflorescentia 1–3; pedunculus 4.5–8 cm longus; spatha 8–20 cm longa; pistilla 5–6-locularia; loculi ca. 19–25-ovulati.

Terrestrial, usually less than 1 m tall, sometimes to 1.5 m, reclining against trees; stem creeping over the ground but well rooted in the soil; internodes 2–4 cm long, 1.5–5 cm diam., pale green to whitish, moderately glossy, usually totally hidden by cataphylls, coarsely but faintly white-short-lineate at apex, drying pale brown, epidermis closely and mostly bluntly ridged with ridges close and cracked transversely; roots moderately few per node, drying 2–3 mm diam., dark brown, closely ridged and weakly scaly; cataphylls 21–29 cm long, unribbed, weakly 1-ribbed or weakly 2-ribbed, whitish to maroon or russet, heavily tinged pink toward lower half, drying dark brown to reddish brown, persisting semi-intact at least toward apex with an underlying network of pale, anastomosing fibers, the outer surface becoming fibrous toward the base. LEAVES erect to erect-spreading; **petioles** 50–56 cm long, 8–19 mm diam., terete or subterete, dark green, tinged purple-violet, weakly glossy, drying dark brown, weakly, obtusely and narrowly sulcate to obtusely flattened adaxially, weakly flattened and often tinged purplish toward apex, faintly striate on surface, sparsely scaly in upper one-third to one-half, scales fine, ± terete, 1–2 mm long, 0.1 mm diam., green; **blades** ovate-cordate, subcoriaceous, moderately bicolorous, acuminate to long-acuminate at apex, prominently cordate at base, 33–65 cm long, 23–36 cm wide, upper surface subvelvety-matte, dark green, drying dark brown, lower surface semiglossy, moderately paler, drying medium yellow-brown; anterior lobe 23–48 cm long, 23–36 cm wide; posterior lobes narrowly rounded, 8–25 cm long, 12–14 cm wide; sinus hippocrepiform, 8–14 cm deep; midrib concave, concolorous or paler above, convex or thicker than broad, much darker olive-green and matte, sometimes tinged maroon near base below, drying darker than surface; basal veins 6–9 per side, with upper 2–3 free to base, part of the remainder coalesced 2–4.5 cm; posterior rib naked for 0.5–3 cm, moderately straight; primary lateral veins (3)5–10 per side, 1.7–2.2 cm apart, departing midrib at a 45–60° angle, downturned acutely at the midrib, weakly sunken to weaky quilted above, convex and darker below, often branching toward the margins, drying blackened; interprimary veins persistent in lower half of blades; minor veins moderately visible but not dis-

tinct when fresh, moderately distinct on drying, weakly undulate, arising from both the midrib and primary lateral veins. INFLORESCENCES 1–3 per axil; peduncle 4.5–8 cm long, to 4 mm diam., pinkish red, coarsely white-lineate toward apex, drying blackened; **spathe** 8–20 cm long, 1–2 cm diam. when furled, to 5.5 cm wide when open (7–11 cm wide when fully flattened), ((2.5)3–3.7 times longer than peduncles), acuminate at apex (acumen 2.5 cm long), semiglossy, in Central America pale yellow-green, darker green toward middle, white along margins, sometimes tinged with pink, the open margin sometimes violet-purple outside, greenish white and matte throughout within, in South America spathe tube sometimes reddish outside, dark red to red-violet, suffused onto lower one-half of blade inside; spathe blade to 15 cm long, white within; spathe tube 7.5–8.5 cm long, to 4.3 cm diam. at anthesis; **spadix** weakly stipitate; 14–15.5 cm long; pistillate spadix (3.4)4–4.3 cm long in front, 2.8–4 cm long in back, 11–16 mm diam. at apex, 1.2–1.8 cm diam. at middle and base; staminate portion 10–13 cm long, 1.2–1.5 cm diam. at base, 1.5–1.8 mm diam. midway, 8–12 mm diam. 1 cm from apex, constricted to 1.5 cm diam. above the sterile portion; sterile staminate portion to 3.4 cm long, 20 cm diam. at base, 10–18 mm diam. at apex; pistils 1.1–2.4(3.5) mm long, 1.2–5 mm diam.; ovary 5–6-locular, with axile placentation; locules 1.3–1.6 mm long; ovules 19–25 per locule, 2–3-seriate, ca. (0.1)0.25–0.3 mm long; funicle as long as or shorter than ovules, ⅓–⅔ as long as the ovule; stigma 1–1.5 mm diam., depressed medially; style similar to style type B, 1 mm diam.; style apex flat to weakly concave; stylar canals arising at base of apical depressions; stigma discoid, 0.8 mm thick, 1.5–18. mm diam.; the androecium truncate to ± prismatic, margins irregularly 4–6-sided, many 6-sided, ca. 0.6 mm long; thecae oblong, ± parallel to one another; sterile staminate flowers clavate, irregularly 4–5-sided to ovoid, 0.9–1.3 mm long.

Flowering phenology in *Philodendron malesevichiae* in Panama is uncertain. All flowering collections are from South America. Flowering collections have been made in February and March and postanthesis collections in March, July, and December. Cultivated collections from Panama grown at the Missouri Botanical Garden flowered in May, June, July, November, and December.

Philodendron malesevichiae ranges from Panama to Colombia. In Panama it is only known from the type locality in *Tropical wet forest* at 830 to 860 m in Coclé Province. In Colombia it has been collected only along the Pacific Coast in Chocó and Valle at 50 to 150 m elevation.

Philodendron malesevichiae is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is characterized by its terrestrial, creeping habit; short internodes; weakly 1–2-ribbed cataphylls drying reddish brown and persisting semi-intact; subterete, narrowly sulcate petioles, which are conspicuously scaly in the upper one-third; and ovate-cordate brown-drying blades with up to eight basal veins, largely coalesced and naked along the hippocrepiform sinus.

This species is most easily confused with *P. glanduliferum.* The latter species differs in having fewer primary lateral veins (2–4 vs. 6–10 for *P. malesevichiae*); posterior ribs that are not at all naked; and a narrow closed or spathulate sinus (vs. hippocrepiform in *P. malesevichiae*).

In Panama there are three other species that have petiolar glands of some form and thus might be confused with *P. malesevichiae.* These are: *P. hammelii, P. verrucosum,* and *P. squamipetiolatum. Philodendron hammelii* differs in its smaller, green-drying blades and petiolar scales mostly less than three times longer than broad. *Philodendron verrucosum* differs in its mostly appressed-climbing habit; scaly cataphylls, inflorescences, and even parts of the lower blade surface; and velvety and matte (rather than semiglossy) upper blade surface. *Philodendron squamipetiolatum* differs in its appressed-climbing habit, long internodes, deciduous cataphylls, green-drying blades, and scaly inflorescences.

Zarucchi & Escheverry 4776, from 2000 m elevation in Antioquia Department, Colombia, may also belong to this species. It is described as having a deep wine-red (rather than green) spathe.

This species is named in honor of Petra S. Malesevich, who has loyally worked with me on all aspects of the *Philodendron* revision. This species is in cultivation at the Missouri Botanical Garden and is deemed a beautiful addition to horticulture.

Additional specimens examined. PANAMA. **Coclé**: La Mesa, above El Valle de Antón, 860–900 m, *Croat 37319* (MO); base of Cerro Gatital, 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76707* (CAS, MO, PMA).

COLOMBIA. **Chocó**: hills above junction of Río Capá and Río Mumbú, up river from Lloró, 80–120 m, 5°37′N, 76°25′W, *Juncosa 1448* (MO). **Valle**: Buenaventura, Bajo Calima region, Buenaventura–Málaga, Km 65–66, 40–65 m, 4°10′N, 77°12′W, *Croat 71057* (COL, MO); 100 m, 4°4′N, 77°09′W, *70162* (CAS, COL, L, MEXU, MO, NY, PMA); Km 49, 150 m, 4°02′N, 77°04′W, *Croat & Bay 75810* (B, CM, COL, F, GB, M, MEXU, MO, PMA, US); Buenaventura–Río Calima, 33.3 km beyond main Cali–Buenaventura Highway, 50 m, 4°02′N, 77°07′W, *Croat 61377* (AAU, COL, MO, PMA, TEX, US); near Km 14

marker, <50 m, 3°56′N, 76°59′W, *Croat 57547* (CM, COL, G, JAUM, MO).

Philodendron mexicanum Engl., in Mart., Fl. Bras. 3(2): 143. 1878. TYPE: Mexico. Veracruz: vic. of Córdoba, *Bourgeau 2176* (holotype, P; isotype, G). Figures 285–288.

Philodendron latisagittium Matuda, Anales Inst. Biol. Univ. Nac. México 22: 371, Fig. 2. 1951. TYPE: Mexico. Chiapas: Mpio. Siltepec, Cascada, mixed humid forest, over humid rocks, 1200 m, 4 Mar. 1951, *Nakamura 31* (holotype, MEXU).

Usually hemiepiphytic, sometimes terrestrial or epilithic; stem scandent, leaf scars conspicuous, 1–1.5 cm long, 1.3–1.6 cm wide; internodes scurfy, glaucous to semiglossy, 18–21 cm long, 1–2 cm diam., longer than broad, medium green to gray-green, epidermis blistering, fissured ± transversely; roots branched at tips, sometimes with swollen nodes along length; cataphylls fleshy, 10–23 cm long, unribbed or bluntly 1-ribbed, pale green, glossy, drying yellowish tan to yellowish green, deciduous intact; **petioles** 22–66.5 cm long, 2–13 mm diam., terete, moderately spongy, medium green, somewhat flattened adaxially, surface semiglossy; **blades** narrowly triangular-sagittate to triangular-hastate, subcoriaceous, acuminate to long-acuminate at apex, sagittate to hastate at base, 23–46 cm long, 14–38 cm wide (1.3–2.7 times longer than wide), (0.6–1.5 times longer than petiole), about equal in length to petiole, margins weakly undulate, upper surface dark green, drying dark brownish green, semiglossy, lower surface drying yellowish green, weakly glossy, paler; medial lobe 19–38 cm long, 8–20 cm wide (1.7–2.7 times longer than posterior lobes), usually 3–3.5 times longer than wide (rarely to 1.7 times longer than wide); posterior lobes 7–19.5 cm long, 4–12.6 cm wide, directed somewhat toward the base, rounded to rarely rounded; sinus parabolic to hippocrepiform or spathulate; midrib broadly sunken, concolorous above, convex, sparsely orange-spotted, slightly paler than surface below; basal veins 0–1(2–5) per side, with 0–1(2–5) free to base, or 1 coalesced, the third and fourth coalesced 3.6–4(13) cm; posterior rib not naked or naked for 0.5–2 cm, directed straight toward the tip of the blade and remaining 1.5–3.5 cm distant from blade margin; primary lateral veins (2)4–5(6) per side, departing midrib at a 55–65° angle, ± straight to the margins, weakly sunken above, raised below; minor veins moderately distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 4–15 cm long, 4–12 mm diam.; **spathe** glossy, 8–16.5 cm long, 1.9–2.3 cm diam. (0.8–1.4(1.5–2.4) times longer than peduncle), acute at apex, the margins paler to clear within; spathe blade greenish to whitish outside; resin canals pale range and appearing as continuous lines inside; spathe tube greenish, sometimes pale reddish tinged outside; red-violet to maroon (B & K red-purple 5/7.5) inside; **spadix** sessile; bluntly rounded to somewhat acute at apex, 10.5–14.7 cm long, broadest toward the apex, constricted below the middle of fertile staminate portion; pistillate portion pale green to green to pale yellow, cylindrical to obovoid, 2–6 cm long, 1 cm diam. at apex, 1.1 cm diam. at middle, 1.3 cm wide at base; staminate portion (6.4)10.3–12.7 cm long; fertile staminate portion creamy white, ± cylindrical, 6–17 mm diam. at base, 7–15 mm diam. at middle, 1.1 cm diam. ca. 1 cm from apex, about as broad as the pistillate and the sterile portions; sterile staminate portion usually broader than the pistillate portion, white to light gray, 1–1.2 cm diam.; pistils 1.6–2(3.5) mm long, 1.1–1.3(2.6) mm diam., transparent white; ovary 5–7-locular, 0.9–2.7 mm long, 1.2–1.4(2.3–2.6) mm diam., with sub-basal placentation; locules 0.9–1.1(2.5) mm long, 0.2–0.4(0.6–0.7) mm diam.; ovule sac 0.6–0.7 mm long; ovules 1–2(3) per locule, digitate, contained within transparent ovule sac, 0.3–0.6(1.1) mm long, longer than funicle; funicle 0.3 mm long, style 0.7(1) mm long, 1.2–1.5(2.4) mm diam., similar to style type B; style apex domed; stigma discoid, at least sometimes lobed both laterally and vertically, sometimes ± cylindrical, 0.7–1.0 mm diam., 0.1–0.3 mm high, covering center of style apex, at least sometimes drying with radial arms sunken between the central peak and the peaks on the end of the arms (*Croat & Hannon 64520*); the androecium truncate, margins irregularly 4–6-sided; thecae ± cylindrical, 0.3–0.4 mm wide, ± parallel to one another; sterile staminate flowers bluntly or acutely 4–6-sided, 1.3–1.9 mm long, 1.3–1.8 mm wide. INFRUCTESCENCE with seeds 1 per locule, yellowish orange, 1.5–1.9 mm long, 0.6–0.8 mm diam.

Flowering in *Philodendron mexicanum* occurs in the mid-dry season and early rainy season (February through May), with post-anthesis collections known February through June (except May) and also in November. Mature fruits are not known. A cultivated collection at Missouri Botanical Garden (*Croat 59933*) flowered perhaps twice per year, in March and in October.

Philodendron mexicanum ranges from Mexico to Colombia, from near sea level to 1900 m elevation, ranging from dry habitats in west-central Mexico (both "Selva Baja Caducifolia" and "Bosque Pino-

Encino") to more humid sites on the Atlantic slope in Vera Cruz to as far south as Honduras in *Tropical moist forest* and to Costa Rica in *Premontane wet forest*. Though widespread, this species is apparently rare and has been collected from relatively few localities, often restricted to mesic enclaves in otherwise arid regions as in the state of Morelos, Mexico. It is one of the most ecologically versatile species in the genus.

Philodendron mexicanum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is recognized by its scandent habit; internodes longer than broad; unribbed, deciduous cataphylls; moderately spongy, somewhat flattened petioles (about as long as the blades); and especially by its narrowly triangular-sagittate to triangular-hastate blades, which dry dark brownish green above and yellowish green below. Sterile collections from Los Ríos and Guayas Provinces of Ecuador (*Dodson & Valverde 6959*) at Jauneche and in Guayaquil Cantón (*Rubio et al. 2008*) may also represent this species. Dodson et al. (1985) erroneously reported the former collection as *P. barrosoanum* G. S. Bunting, a species restricted to the eastern side of the Andes.

Philodendron mexicanum is most similar to *P. angustilobum*, a species ranging from Honduras to Panama. The latter species differs in having leaves that dry more blackened (rather than green to yellow-green as in *P. mexicanum*), and which are more decidedly three-lobed with the medial lobe proportionately narrower and broadest at the middle or even above the middle.

Although the type specimen of *P. mexicanum* was collected in Mexico near Córdoba, most Mexican collections are from the Pacific slope. These have somewhat less prominently narrowed posterior lobes than the type. *Moore & Bunting 8873*, from near the type locality, has the posterior lobes even more conspicuously narrowed than those of the type specimen. In this regard, its blades approach those of *P. angustilobum* in overall shape, but differ in drying greenish to yellowish brown rather than blackened.

A collection from Olancho Department, Honduras (*Croat & Hannon 64520*), is unusual in having a style that dries with radiating arms from a central peak.

The sole Costa Rican collection (*Grayum 5418*) is unusual in having prominently hastate blades. This collection has only a juvenile inflorescence. Further collections may prove it represents a distinct species.

Additional specimens examined. COSTA RICA. **Puntarenas**: Río Guacimal downstream from Monteverde, Cordillera de Tilarán, 1300 m, 10°18′N, 84°49′W, *Grayum 5418* (MO). GUATEMALA. **Quezaltenango**: Finca Pireneos–Patzulín, 1200–1400 m, *Standley 86917* (F); *87007* (F); *87022* (F). **San Marcos**: Volcán Tajumulco, 1300–1500 m, *Steyermark 37968* (F). HONDURAS. **Atlántida**: Quebrada Grande, ca. 10 km SW of La Ceiba, 80–180 m, 15°42′N, 86°51′W, *Liesner 26138* (MO). **Olancho**: San Esteban–Bonito Oriental, Río Grande, 350–400 m, 15°31′N, 85°42′W, *Croat & Hannon 64520* (B, CAS, CM, CR, HNMN, K, L, MEXU, MO, NY, USCG). **Yoro**: Puente Grande, Río Puente Grande (tributary of the Río Agua), *Blackmore & Chorley 4077* (BM, MO). MEXICO. Cultivated at Cornell University, Ithaca, New York, *Moore 7437* (BH); Ixtapan de La Sal, 1900 m, 18°50′N, 99°41′W, *Matuda et al. 32130* (MEXU). **Guerrero**: Atoyac region, above Fila de Caballo, El Paraíso in Parque Nacional de Guerrero, *Croat 67442* (MO). **Morelos**: Cuernavaca, *Bourgeau 1420* (K, P); 1350 m, *Quarles van Ufford 95* (U); 5000 ft., *Pringle 8093* (BH, BM, BR, CM, F, G, GH, H, HBG, ISC, K, LL, MASS, MEXU, MO, NY, P, POM, RSA, UC, US); *Rose & Hough 4439* (US); Río Pollo, below Salto San Antonio, Fraccionamiento San Antonio, W of Colonia Carolina, NW of Center of Cuernavaca, 1500 m, 18°57′N, 99°15′W, *Croat & Hannon 65778* (B, CM, F, GH, K, MEXU, MO, NY, US); *Matuda 26030* (MEXU); *25982* (F, MEXU); *Moore & Bunting 8820* (BH); Barranca Santa Clara, N de Acatlipa, 1450–1550 m, *Vázquez 3094* (MEXU). **Veracruz**: Córdoba–Veracruz, Ejido San José de Gracia, below Peñuelo, ca. 730? m, *Moore & Bunting 8873* (BH, MO).

Philodendron microstictum Standl. & L. O. Williams, Ceiba 3: 108–109. 1952. TYPE: Costa Rica. Puntarenas: Esquinas Forest Reserve, sea level, 10 Jan. 1951, *Allen 5755* (holotype, EAP; isotypes, F, GH, US). Figures 289, 290.

Hemiepiphytic vine, stem scandent, green to gray-green, drying pale yellowish brown, unscented, leaf scars inconspicuous, 1.2 cm long, 8 mm wide, obscured by cataphylls; internodes smooth, semiglossy, 6–12 cm long, 1–2 cm diam., longer than broad, moderately green, drying khaki-colored, epidermis fissured transversely; roots drying light reddish brown, smooth, weakly glossy, 20–30 cm long, 2–3 mm diam., 4–6, at the nodes; cataphylls subcoriaceous, bluntly 2-ribbed or unribbed, pale green to cream-colored, promptly deciduous; **petioles** 12–24 cm long, 2–4 mm diam., subterete to broader than thick to broadly D-shaped, weakly spongy, bluntly flattened to broadly sulcate adaxially, rounded abaxially, with adaxial margins blunt, surface pale or dark green streaked and demarcated from blade by dark green ring around apex; **blades** broadly ovate, moderately coriaceous, abruptly acuminate at apex (the acumen tightly inrolled, 1–4 mm long), weakly subcordate at base, 12.5–30 cm long, 13–21.5 cm wide (0.7–1(1.7) times longer than wide), (0.65–2 times longer than petiole), about equal in length to petiole, broadest ± near the middle, margins straight, upper surface dark green, semiglossy, somewhat pruinose, lower sur-

face glossy to weakly glossy, paler; anterior lobe 12–20.5 cm long, 10.7–22 cm wide (1.85–3 times longer than posterior lobes); posterior lobes 4–8 cm long, 3.5–9.5 cm wide, broadly rounded to obtuse; sinus arcuate, sometimes parabolic, 3.4–6 cm deep; midrib broadly convex to weakly raised, concolorous to paler than surface above, weakly to broadly convex, paler than surface below; basal veins about 3 per side, obscurely and scarcely more conspicuous than primary laterals; posterior rib lacking; primary lateral veins (3)4–5 per side, obscure above; minor veins about as conspicuous as the primary laterals, arising from the midrib only. INFLORESCENCES spreading, as long as leaves, 1 per axil; peduncle 14–25 cm long, 2–6 mm diam., subterete, green; **spathe** 6.5–15 cm long (0.3–1 times longer than peduncle); spathe blade green outside, pale green inside; spathe tube ca. 5 cm long, green outside, red or violet-purple inside; **spadix** sessile, 8 cm long, broadest below the middle; pistillate portion medium green to pale greenish yellow, ± cylindrical, 1.9–2 cm long, 6.5–7 mm diam. at apex, 7–8 mm diam. at middle, 6.5–7 mm wide at base, with 13 (per cm) flowers per spiral; staminate portion 5.9–8.3 cm long; fertile staminate portion white, tapered toward apex, 5–9 mm diam. at base, 5–6 mm diam. at middle, 0.9 mm diam. ca. 1 cm from apex, broadest at the base, mostly narrower than the pistillate and sterile portions; sterile staminate portion broader than the pistillate portion, 6–9 mm diam.; pistils 1.2–1.4 mm long, 0.8–1.1 mm diam.; ovary 6–7-locular, 0.8–1 mm long, 0.8–1.1 mm diam., with sub-basal placentation, walls drying weakly warty; locules 0.8 mm long, 0.3 mm diam., ovule sac 0.7–0.8 mm long; ovules 1 per locule, contained within transparent ovule sac, 0.4 mm long, as long as funicle; funicle 0.4 mm long; style 0.2 mm long, 1 mm diam., similar to style type B; style apex flat; stigma unlobed, subdiscoid to somewhat cylindrical, 0.8–0.9 mm diam., 0.2 mm high, covering almost entire style apex, centered on stylar canal pores; the androecium truncate, margins irregularly to bluntly 4–6-sided, 1.2 mm long, 0.8 mm diam. at apex; thecae ± cylindrical, 0.3 mm wide, ± parallel to one another, contiguous; sterile staminate flowers acutely or bluntly and irregularly 4–6-sided, 1.2–2 mm long, 0.7–1.1 mm wide. INFRUCTESCENCE with fruits whitish. Seeds (dried) ca. 20 per locule, tan, 1–1.2 mm long, 0.5–0.6 mm diam., finely ridged with much finer cross-etching.

Flowering in *Philodendron microstictum* occurs during the dry season and early rainy season, with flowering collections known from January, April, and May, and post-anthesis collections from February, March, May, and July. Immature fruits have been collected in May.

Philodendron microstictum is endemic to Costa Rica (though to be expected on the Burica Península in adjacent Panama), where it is restricted to the Pacific slope, at 50 to 450 m elevation in wetter parts of *Tropical moist forest*, *Tropical wet forest*, and *Tropical wet forest* basal belt transition life zones.

Philodendron microstictum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is characterized by its scandent habit; long, moderately slender stems drying pale yellowish brown; subterete petioles, which are about as long as the blades; and broadly ovate, weakly subcordate blades (which may be as wide or wider than long) with an arcuate sinus and obscure primary lateral and basal veins (sometimes with only the basal veins visible). Also characteristic is the externally green spathe (red within the tube) with the peduncle as long as or longer than the petiole.

Philodendron microstictum is not easily confused with any other species. It has been confused by some with *P. scandens*, which differs in having more narrowly ovate blades with prominent major veins and a spathulate to parabolic sinus, and much more short-pedunculate inflorescences (with the peduncles much shorter than the petioles).

This species is perhaps related to *P. chirripoense*, which is also a vine with inflorescences longer than leaves and has blades of similar color and texture. That species differs in having longer, more slender internodes that dry dark brown and by its narrowly ovate, subcordate blades, which are more than twice as long as broad and have more prominent primary lateral veins.

Additional specimens examined. COSTA RICA. **Puntarenas**: Palmar Norte, 100–200 m, *Croat 35107* (CR, MO); Palmar Norte, along trail to Jalisco, 50–700 m, *Croat 35189* (F, MO); 110 m, *Croat & Hannon 79210* (CR, INB, MO); Villa Neily–San Vito de Coto Brus, Cuesta Fila de Cal, 300 m, 8°41′N, 82°57′W, *Grayum et al. 7580* (CR, MO); El General Valley, Río Angel–Río Volcán, 450–500 m, *Williams et al. 24214* (CR, F); Osa Península, 20–300 m, *Liesner 1836* (B, MO); ca. 5 km W of Rincón de Osa, 50–200 m, 8°42′N, 83°31′W, *Burger & Liesner 7300* (CR, F, MO, PMA); Fila Huacas, ca. 4 km NE of Las Huacas ('Venecia') along road to Sinaí, 450–500 m, 8°52′N, 83°17′W, *Grayum & Hammel 10132* (CR, MO); Parque Nacional Corcovado, La Palma, 100 m, 8°35′N, 83°30′40″W, *Herrera 4066* (CR, L, MO, NY); Sirena, 0–150 m, 8°27–30′N, 83°33–38′W, *Kernan 463* (CR); in Monkey Woods (just W of airstrip), 5 m, 8°29′N, 83°35′W, *Hammel et al. 16643* (CR, MO); Claro Ridge, 1–10 m, 8°28′N, 83°35′W, *Kernan & Phillips 1028* (CR, MO); Sirena Woods, 1–50 m, 8°28′N, 83°35′W, *Kernan & Phillips 1089* (CR, MO); Río Sorpresa, ca. 1 km NE of Golfito, E of microwave towers, ca. 400 m, 8°39′N, 83°10′W, *Croat & Grayum 59941* (CR, MO); Golfito, Cerro Las Torres, 500

m, *G. Herrera 5045* (CR, INB, MO); Reserva Forestal Golfo Dulce, W of Rancho Quemado, 1–300 m, 8°44′N, 83°36′W, *Saborío et al. 127* (INB, MO); Río Volcán, 48 km SE of San Isidro General, 300 m, *Molina et al. 18162* (F, GH, NY, US). **San José**: Río Negro, ZP La Cangreja, ca. 1.5 km E of Santa Rosa de Puriscal, 320 m, 9°42′N, 84°23′30′W, *Grayum et al. 8340* (MO); Parque Nacional, sector Esquinas, vic. Fila Gamba, 200–300 m, *Croat & Hannon 79288* (MO).

Philodendron morii Croat, sp. nov. TYPE: Panama. Panamá: Valle de Madroño, ca. 10 mi. N of La Margarita (near Chepo), in forest S of and on Continental Divide, near border of Comarca de San Blas, along trial to Cangandí, 350–450 m, 9°19′N, 79°08′W, 21 Feb. 1986, *Hammel & McPherson 14530* (holotype, MO–3398570). Figures 291, 292.

Planta epiphytica; internodia 1–1.5 cm longa, 1.5–2 cm diam.; cataphylla 13 cm longa, obtuse 2-costata, decidua; petiolus subteres, 23–37 cm longus, (2)4–6 mm diam., subspongiosus; lamina ovato-triangularis, leniter cordata basi, 25–27.5 cm longa, 11.5–16 cm lata, in sicco canaviridis; inflorescentia 2; pedunculus 9.5–14 cm longus, 3–6 mm diam.; spatha 8.7–12 cm longa, viridis vel flavividis omnino; pistilla (3)4–5(6)-locularia; loculi cum 3–6 seminibus; baccae albae.

Epiphytic; stem appressed-climbing; internodes semiglossy, 1–1.5 cm long, 1.5–2 cm diam., about as long as broad, dark green, drying light brown; roots drying reddish brown; cataphylls 13 cm long, bluntly 2-ribbed, green, deciduous, intact; **petioles** 23–37 cm long, (2)4–6 mm diam., subterete, somewhat spongy, dark green, obscurely flattened adaxially, surface unmarked, often dries with loose, puffy epidermis; **blades** ovate-triangular, narrowly acuminate at apex, weakly cordate at base, 25–27.5 cm long, 11.5–16 cm wide (1.7–2.4 times longer than wide), (0.7–1.2 times longer than petiole), about equal in length to petiole, upper surface semiglossy, lower surface drying green, weakly glossy, moderately paler; anterior lobe 24–28 cm long, 12.6–16 cm wide; posterior lobes broadly rounded, 5–7 mm long, 3–7.5 cm wide, broadly rounded to obtuse; sinus arcuate with blade decurrent on petiole; midrib prominently raised above, slightly paler than surface below; basal veins 2–3 per side, with 0–1 free to base, 0–1 coalesced less than 1 cm; posterior rib weak, to 1.3 cm long, naked throughout its length; primary lateral veins (2)5–8 per side, departing midrib at a 40–50° angle, straight to the margins, sunken and concolorous above, convex and darker than surface below; minor veins fine, numerous, and distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES (post-anthesis) 2 per axil; peduncle 9.5–14 cm long, 3–6 mm diam.; **spathe** 8.7–12 cm long, (0.8–1.1 times longer than peduncle), green to yellowish green throughout; spathe tube 3.5–5 cm long; **spadix** 8–11 cm long; pistillate portion (post anthesis) 5.7 cm long in front, 4.8 cm long in back, 1.5 cm diam. midway, 1.2 cm diam. near apex, 8 mm diam. near base; fertile staminate portion 5 cm long, narrowly tapered to apex, the narrowest portion to 5 mm diam., ca. 1.3 cm above base; sterile staminate portion broader than constricted area, to 5.5 mm diam.; pistils 1.4–1.6 mm long; ovary (3)4–5(6)-locular, with sub-basal placentation; locules 1.3 mm long, 0.5 mm diam.; ovules 1 per locule, 0.3 mm long; funicle 0.2–0.3 mm long (can be pulled free to base), style similar to style type D; style apex flat to weakly rounded, 0.6–0.7 mm long, style boss small; stigma covering entire style apex and inserted on style boss; the androecium truncate, margins irregularly 4–6-sided, 0.7 mm long. INFRUCTESCENCE with pistillate spadix 3–5 cm long; berries white, ± oblong-ellipsoid, 1.1–2 mm long, 0.4–0.8 mm diam.; seeds 3–6 per locule, tan.

Flowering phenology in *Philodendron morii* is poorly known, but it is perhaps bimodal with flowering collections known in March and November and immature fruits in December, February, and June.

Philodendron morii is endemic to Panama, known only from highlands east of the Canal Area in Panamá Province and Comarca de San Blas and from Cerro Pirre in Darién Province, at 450 to 850 m elevation in *Tropical wet forest* and *Premontane rain forest* life zones.

Philodendron morii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is characterized by its slender internodes (about as long as broad); bluntly two-ribbed, deciduous cataphylls; terete petioles (about as long as the blades), which often dry with loose, puffy epidermis; ovate-triangular, scarcely cordate, green-drying blades; and peduncles equaling or exceeding the green spathes.

Philodendron morii is most similar to *P. sphalerum* Schott from the Guianas, which has similar green-drying, long-petiolate leaves. The latter species differs in having the leaf blades acute to rounded or truncate at the base and proportionately longer petioles (fully as long as or much longer than the blades). In addition, *P. sphalerum* has up to four much smaller inflorescences with spathes 5.5–7 cm long, whereas *P. morii* has one to two much larger inflorescences per axil (spathes 9–12.5 cm long). *Philodendron morii* is also similar to *P. wilburii*, especially in terms of size and color of its leaf

blades. The latter species differs, however, in comprising more or less scandent plants with usually long internodes.

Philodendron morii is not easily confused with any other Central American species. It is named in honor of one of its earliest collectors, Scott Mori (NY), who collected for the Missouri Botanical Garden during 1974–1975.

Additional specimens examined. PANAMA. **Darién**: Parque Nacional Darién, W side of Cerro Pirre, 800–1050 m, 7°56′N, 77°45′W, *Croat 68700B* (MO). **Panamá**: Cerro Jefe region, Altos de Azul–Río Chagres, 700–850 m, 9°15′N, 79°30′W, *McPherson 11899* (MO, PMA, US); 3–3.5 mi. NE of Altos de Pacora, 11.1–11.6 mi. beyond Lago Cerro Azul, 700–750 m, 9°15′N, 79°25′W, *Croat 68693* (CM, MO); Campos Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Liesner 567* (MO); Gorgas Memorial Labs "Campamento Quatro," 5–10 km NE of Altos de Pacora, ca. 600 m, *Mori & Kallunki 3441* (MO). **San Blas**: Río Diablo, Cordillera de Ibedón, 350–480 m, 9°21′N, 78°34′W, *Herrera et al. 1489* (MO, PMA, US).

Philodendron niqueanum Croat, sp. nov. TYPE: Panama. Darién: Serranía de Pirre, along headwaters of Río Escucha Ruido, ca. 16 km due N of Alto de Nique, ca. 7°47′N, 77°45′W, 27 July 1976, *Croat 37942* (holotype, MO–2416709). Figures 293–296.

Planta hemiepiphytica; internodia brevia, usque 5 cm diam.; cataphylla incostata vel leniter 1-costata, rubra, persistentia plus minusve intacta; petiolus teres, (32)46–59 cm longus, in sicco 6–8 mm diam.; lamina ovata vel late ovata, (28)42–55.5 cm longa, (14)25–28.5 cm lata, circa tam longa quam petioli; sinus plus minusve V-formatus; inflorescentia immatura; pedunculus 4 cm longus; spathae virides.

Hemiepiphytic; stem scandent when young, appressed-climbing when adult; internodes short, to 5 cm diam. (younger stems with internodes to 8 cm long, 1.5 cm diam.), epidermis moderately smooth, dark reddish brown; cataphylls unribbed to weakly 1-ribbed, red, persisting ± intact; **petioles** (32)46–59 cm long, 6–8 mm diam., terete; **blades** ovate to broadly ovate, acuminate at apex, truncate to subcordate at base, (28)42–55.5 cm long, (14)25–28.5 cm wide (1.7–2 times longer than wide), (ca. 0.9 times the petiole length), about equal in length to petiole, upper surface weakly glossy, drying dark brown, lower surface paler, drying dark yellowish brown; anterior lobe (27)37–49.5 cm long, 25–28.5 cm wide (4.7–5.4(13.5) times longer than posterior lobes); posterior lobes (2)7–9 cm long, 9–12 cm wide, broadly rounded to obtuse; sinus ± V-shaped, to 4 cm deep; midrib prominently raised, paler than surface above, raised below; basal veins 3 per side, with 0 free to base, some of the lowermost coalesced to ca. 1 cm; posterior rib never naked; primary lateral veins 5–9 per side, departing midrib at a 45–65°(70°) angle, weakly arcuate to the margins, sunken above, raised below; minor veins obscurely visible, slightly raised on drying below, arising from the midrib only. INFLORESCENCES immature; peduncle 4 cm long; **spathe** green, 7 cm long; **spadix** immature.

Flowering in *Philodendron niqueanum* is poorly known owing to too few collections overall. The species was collected with flower buds in late July and probably both flowers and fruits within the rainy season (although, since it flowers so late, the fruits may mature in the dry season).

Philodendron niqueanum is endemic to Panama, known only from the type locality on the Serranía de Pirre, at 1530 to 1550 m elevation in *Tropical Lower Montane wet forest.*

Philodendron niqueanum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Ecordata.* This species is characterized by its thick, short internodes; red, weakly one-ribbed cataphylls persisting mostly intact; terete petioles; and narrowly ovate, dark brown-drying blades about as long as the petioles.

Philodendron niqueanum is apparently close to *P. lentii,* which ranges from Costa Rica to central Panama, but no further east than the province of Coclé. Both species are similar in having truncate- to subcordate-based leaf blades with more or less V-shaped sinuses. *Philodendron lentii* differs in having the primary lateral veins sunken, paler, and much more conspicuous on the upper dried blade surface. In contrast, the primary lateral veins of *P. niqueanum* are scarcely or not at all paler than the surface on dried leaves and are raised rather than sunken. In addition, the epidermal pattern is alveolate and moderately smooth at 10× magnification on the upper blade surface of *P. niqueanum,* whereas *P. lentii* lacks an alveolate pattern and the adaxial surface is densely covered with round, pale inclusions.

Philodendron niqueanum is named for the type locality near the Alto de Nique, hence the name.

Additional specimen examined. PANAMA. **Darién**: Cerro Pirre region, ca. 9 km from Alto de Nique, 1480–1520 m, *Croat 37886* (MO, PMA, US).

Philodendron panamense K. Krause, in Engl. & K. Krause, Pflanzenr. IV. 23Db (Heft 60): 65. 1913. TYPE: Panama. Canal Area: at Frijoles, 25–30 m, 9°10′N, 79°48′W, *Pittier 3753* (holotype, US). Figures 297–299.

Usually hemiepiphytic; stem appressed-climb-

ing, to 1.3 m long, sap reddish, sticky; internodes short, semiglossy, 2.5–4 cm diam., sometimes longer than broad, dark green; roots several per node, drying 2–4 mm diam., dark brown, semiglossy, sparsely scaly; cataphylls 18–20 cm long, sharply 1-ribbed to sharply 2-ribbed, green to whitish, drying light brown, persisting briefly ± intact, eventually fibrous, sometimes persisting for a time, eventually deciduous; **petioles** erect-spreading, (23)34–70(79) cm long, 4–13 mm diam., terete to subterete, sometimes weakly flattened or with narrow flattened rib adaxially, sometimes weakly and narrowly sulcate at base, dark green, sometimes pink at base, surface sparsely to densely pale greenish striate or striate-lineate, minutely grooved upon drying, geniculum to 6.5 cm long, sheath 1–4 cm long, usually inconspicuous, to 10 cm long when subtending an inflorescence; **blades** broadly triangular-ovate or more infrequently ovate, subcoriaceous, semiglossy, moderately bicolorous, abruptly acuminate, sometimes acute at apex (the acumen sometimes inrolled, to 4 mm long), deeply cordate at base, 32–72 cm long, 24–38 cm wide (1.2–2.3 times longer than wide, averaging 1.5), ((0.3)0.7–1.4 times longer than petiole, averaging 1.07), broadest near point of petiole attachment; upper surface dark green and glossy, drying semiglossy, dark gray-brown to olive-green, often somewhat blackened, lower surface slightly paler, semiglossy; margins sometimes broadly undulate; anterior lobe 25–41(58) cm long, (15)20–36(41) cm wide (1.9–4 times longer than posterior lobes); posterior lobes 7.5–18 cm long, 4.5–17.7 cm wide, rounded to broadly rounded to broadly obtuse; sinus hippocrepiform to parabolic (arcuate on younger blades), 4–12 cm deep; midrib broadly sunken, concolorous or paler than surface above, weakly asperous, thicker than broad, matte, sometimes short-white-striate, darker than surface below; basal veins 5–8 per side, with 1 free to base or nearly so, third and higher order veins coalesced 4–7 cm long; posterior rib naked for 2–3 cm long; primary lateral veins 4–7 per side, departing midrib at a 55–65° angle, spreading to a 65–75° angle, usually curved down gradually before merging with the midrib, narrowly sunken, concolorous or paler than surface above, convex, matte, slightly darker than surface below; interprimary veins narrowly sunken above; minor veins distinct, darker than surface below, arising from both the midrib and primary lateral veins; secretory ducts moderately visible on lower dried surface, alternating with minor veins. INFLORESCENCES ± erect, 4(6) per axil; peduncle (4.5)6.5–20 (most more than 15) cm long, 4–12 mm diam., pale green, strongly white-lineate, slightly to moderately bent just below the spathe; **spathe** 10.5–18.5 cm long, (0.6–1.7(2.7) times longer than peduncle), acute at apex; spathe blade white outside, (opening 4–7.5 cm wide), pale green, moderately glossy to pale-punctate inside; spathe tube ellipsoid, medium green, densely pale-speckled outside, 6–9 cm long, to 4.5 cm diam., pale green, moderately glossy to pale-punctate inside, **spadix** sessile; protruding forward at anthesis, 12–16 cm long, broadest at upper two-thirds constricted to ca. 1.5 cm diam. between sterile staminate portion and fertile staminate portion; pistillate portion pale green, cylindrical, 3–6.5 cm long in front, 2.7–3.6 cm long in back, 1.3–1.7 mm diam. at apex, 1.3–1.9 mm diam. at middle, 1.1–1.5 mm wide at base; staminate portion 10.5–14.7 cm long; fertile staminate portion creamy white, ± clavate, 1.5–1.8 cm diam. at base, 1.3–2 cm diam. at middle, 9–12 mm diam. ca. 1 cm from apex, about as broad as the pistillate portion; sterile staminate portion 1–1.9 cm diam.; pistils 2.1–3.4 mm long, 1–1.6 mm diam.; ovary 6(7)-locular, 1.5–3.1 mm long, 1–1.6 mm diam., with axile placentation, walls sometimes embedded with granular, crystal-like particles; locules 1.5–3 mm long, 0.5–0.7 mm diam.; ovules 20–31 per locule, 2-seriate, 0.3 mm long; funicle 0.2 mm long, adnate to lower part of partition, style 0.5–0.6 mm long, 1.3–1.6 mm diam., similar to style type B; style apex rounded or domed; stigma truncate, hemispheroid, 1–1.3 mm diam., 0.3–0.5 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins acutely and regularly 4–6-sided, 0.9–1 mm long, 0.7–2.2 mm diam. at apex; thecae oblong to cylindrical, 0.3–0.5 mm wide, ± parallel to one another, contiguous; sterile staminate flowers bluntly, irregularly 4–6-sided, 1.9–4.1 mm long, 1.1–2 mm wide. INFRUCTESCENCE with seeds many per berry, white, narrowly cylindrical, 1.3 mm long, sticky. JUVENILE petioles terete, sheathing broadly, for ½ to ¾ its petiole length, acute to rounded, eventually weakly to strongly cordate; blades broadest at the middle.

Flowering in *Philodendron panamense* occurs during the dry season and early rainy season (March through May), with post-anthesis inflorescences collected from May through August and immature fruits from July through November.

Philodendron panamense is endemic to Panama, but it is likely to occur also in adjacent Colombia. In Panama, it occurs in *Tropical moist forest* on both slopes of the Canal Zone, and *Premontane wet forest* and *Tropical wet forest* in Panamá, Colón, and Da-

rién Provinces, at sea level to 800 m elevation (but mostly below 300 m).

Philodendron panamense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa*. *Philodendron panamense* is characterized by its appressed-climbing hemiepiphytic habit; short internodes; weakly one-ribbed, mostly deciduous cataphylls (sometimes persisting intact or as fibers); terete, pale-striate petioles; usually broadly triangular-ovate, moderately thin blades with parabolic to hippocrepiform sinus; and by the long-pedunculate spathes with externally greenish tube and white blade (greenish white throughout within). Also characteristic is the peduncle, which is often bent abruptly just beneath the spathe.

This species is most easily confused with *P. lazorii*, which has similar greenish inflorescences. The latter species differs in having more broadly ovate blades (0.97–1.4 times longer than wide and averaging 1.1 times) matte on the lower surface. In contrast, the blades of *P. panamense* are usually ovate-triangular, 1.3 or more times longer than broad (averaging 1.5 times longer) with the lower surface semiglossy. In addition, the peduncles of *P. lazorii* are proportionately shorter and usually shorter than the spathe (vs. often longer than the spathe in *P. panamense*).

Philodendron panamense has been confused with *P. jodavisianum*, which has leaves drying a similar, somewhat blackened color. The latter species differs, however, in having D- to U-shaped petioles, typically with a medial rib adaxially, as well as more typically persistent cataphyll fibers and much shorter peduncles (typically less than 10 cm long in *P. jodavisianum*, vs. typically more than 10 cm long in *P. panamense*). In addition, the peduncles of *P. jodavisianum* are usually straight, not bent.

A collection from the Serranía del Pirre at Cana, *Croat 37600*, is unusual in having several persistent cataphylls and shorter-than-usual peduncles.

Collections from Cerro Sapo and Cerro Pirre (*Croat 55184* and *68951* respectively) differ from typical material of *P. panamense* in having ovate (rather than triangular ovate) leaves and more short-pedunculate inflorescences. In addition, they have sharply two-ribbed cataphylls that persist intact (in the case of *Croat 55184*, on plants in the living collection at MO) or semi-intact (*Croat 68951*, collected in the wild on Cerro Pirre). Most dried collections of *P. panamense* have no cataphylls and longer peduncles.

Earlier (Croat, 1978), the species was reported to be much more widely distributed (to Honduras and Ecuador), but collections from outside of Panama have since proven to be misidentified (most now *P. jodavisianum*).

Additional specimens examined. PANAMA. **Canal Area**: Barro Colorado Island, *Croat 5101* (MO); *5530* (MO); *5840* (F, MO, SCZ); *6188* (MO); *8819* (MO, PMA); *8993* (MO); *9292* (MO, PMA, SCZ); *10083* (MO, SCZ); *10264* (MO, SCZ, US); *10819* (MO); *10894* (MO); *11016* (MO); *14876* (MO); *Bailey & Bailey 199* (BH); Parque Nacional Soberania, Pipeline Road, N of Gamboa, *Luteyn & Foster 1556* (MO); Río Macho bridge, 10 km NW of Gamboa, 115 m, *Nee 7869* (MO, US); 6 mi. N of Gamboa, Río Mendoza, 9°11′N, 79°46′W, *Croat & Zhu 77084* (MO); Summit Gardens, *Croat 10867* (F, MO). **Colón**: Portobelo–Nombre de Dios, 0.5 mi. beyond junction of road to Isla Grande, 9°40′N, 79°35′W, *Croat 49804* (MO); near Nuevo Tonosí, <100 m, *Croat 33517* (MO, RSA). **Darién**: Cerro Sapo, *Croat 55184* (AAU, K, MEXU, MO, PMA, US); ca. 5 km S of Garachiné, Río San Antonio, 130 m, 7°59′N, 78°25′W, *Hammel et al. 1481* (MO); Cerro Pirre region, NW of Cana, 600 m, *Sullivan 672* (MO); vic. of gold mine at Cana, 500–600 m, *Croat 37600* (MO); Serranía Sapo above Casa Vieja along boundary trail of Darién National park, 150–300 m, 7°58′N, 78°23′W, *McPherson et al. 15359* (COL, F, MO, NY, PMA), 550–830 m, *15378* (MO, US); Parque Nacional Darién, vic. of Cerro Pirre base camp, trail E side of Río Paracida, 0–80 m, 8°N, 77°48′W, *Croat 68991* (CM, L, MEXU, MO, PMA, US); Estación Rancho Frío, at N base of Cerro Pirre, ca. 9 km S of El Real, 70–270 m, 8°01′N, 77°44′W, *Hammel et al. 16131* (MO); Cerro Pirre, 800–1050 m, 7°56′N, 77°45′W, *Croat 68951* (CAS, COL, MO, NY, PMA); Río Tuquesa, ca. 2 km air distance from Continental Divide, vic. of Tyler Kittredge gold mine, *Croat 27193* (MO); Parque Nacional Cerro Pirre, Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77100* (CAS, CM, F, MO). **Panamá**: road to Cerro Azul, Mile 5, *Croat 11515* (F, MO, PMA); 720 m, 9°04′N, 79°29′W, *Croat 75152* (CM, MO); Cerro Campana, *Dwyer et al. 4848* (MO), *Croat 12074* (MO, SCZ).

Philodendron pirrense Croat, sp. nov. TYPE: Panama. Darién: Cerro Pirre, middle slopes on western approach, 800–1050 m, 7°56′N, 77°45′W, 29 June 1988, *Croat 68952* (holotype, MO–3610823–24; isotypes, B, COL, F, K, NY, PMA, US). Figures 301–305.

Planta hemiepiphytica aut terrestris; internodia 1–2 cm longa, 4–5 cm diam.; cataphylla 25–30 cm diam., acute 2-costata, persistentia ut fibrae grossae pallidae, cum frustris rubrobrunneis epidermidis; petiolus 56.5–100 cm longus, 5–8 mm diam., aliquantum complanatus adaxialiter cum costa inconspicua; lamina late ovato-cordata, 35–58 cm longa, 27–46 cm lata, in sicco brunnea; costa postica nuda 1–5 cm; inflorescentia 4; pedunculus manifeste albostriatus, 8.5–12 cm longus, 6–8 mm diam.; spatha 12–16.7 cm longa; lamina spathae extus viridis, suffusa marronina, intus alba suffusa marronina; tubo spathae extus rubrimarronino, intus atrimarronino; pistilla 5–6-locularia; loculi 20-ovulati; baccae albae.

Hemiepiphytic or sometimes terrestrial; stem to 5 cm long; internodes short, semiglossy, closely ribbed, completely enclosed in cataphyll fibers,

1–2 cm long, 4–5 cm diam.; roots to ca. 30 cm long, drying reddish brown, smooth, semiglossy, ca. 2 mm diam., closely ridged; cataphylls 25–30 cm long, sharply 2-ribbed (ribs prominently raised), reddish, drying reddish brown, persisting semi-intact, ultimately as coarse pale fibers with fragments of reddish brown epidermis; **petioles** 56.5–100 cm long, 5–8 mm diam., subterete, somewhat flattened near base, weakly flattened toward apex, with faint medial rib adaxially, surface densely short-lineate; **blades** broadly ovate-cordate, acuminate to narrowly acuminate at apex, cordate at base, 35–58 cm long, 27–46 cm wide (1.2–1.5 times longer than wide), (0.6–0.9 times longer than petiole), upper surface drying reddish brown, semiglossy, lower surface much paler; anterior lobe 24.5–48.5 cm long, 27–50 cm wide (1.7–2.3 times longer than posterior lobes); posterior lobes ± rounded, 12.5–19 cm long, 12.5–23.5 cm wide, broadly obtuse; sinus hippocrepiform, 14 cm deep; midrib flat, paler than surface above, drying reddish brown below; basal veins 7–11 per side, with 0–1 free to base, 1–2 coalesced (4)6–8(10) cm, posterior rib well developed, naked for 1–5 cm; primary lateral veins 6–10 per side, departing midrib at a 55–65° angle, ± straight to the margins, prominently sunken above, prominently raised below; interprimary veins distinct, fine, mostly continuous, drying darker than surface below; minor veins arising from both the midrib and primary lateral veins. INFLORESCENCES 4 per axil; peduncle 8.5–12 cm long, 6–8 mm diam., prominently white-striate, clearly demarcated from spathe; **spathe** 12–16.7 cm long (1.3–1.5 times longer than peduncle), moderately constricted above the tube; spathe blade green, tinged maroon, conspicuously and densely pale lineate-striate outside, white, tinged maroon inside; spathe tube red-maroon, inconspicuously short-lineate outside, 4–6 cm long, dark maroon inside; **spadix** sessile; ± ovate, 11–13.4 cm long, broadest below the middle; pistillate portion greenish white, 2.7 cm long, 1.4 cm diam. at apex, 1.3 cm wide at base; staminate portion 10.8 cm long; staminate portion 5.7–8.3 cm long; fertile staminate portion white, tapered toward apex, 1.4 cm diam. at base, 1.3 cm diam. at middle, 8 mm diam. ca. 1 cm from apex, broadest at base, about as broad as pistillate portion; sterile staminate portion broader than the pistillate portion, 1.4–1.5 cm diam., pistils 2.5 mm long, 1.2–1.4 mm diam.; ovary 5–6-locular, 1.7 mm long, 1.3 mm diam., with axile placentation, walls embedded with granular, crystal-like particles; locules 1.7 mm long, 0.4 mm diam.; ovules 20 per locule, 2-seriate, contained within gelatinous matrix (no true envelope), 0.2–0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, style 0.3 mm long, 1.3 mm diam., similar to style type B; style apex flat; stigma subdiscoid to slightly hemispheroid, weakly lobed, 1.2 mm diam., 0.1–0.3 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided; thecae oblong, 0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregular, 4–6-sided, 2.1–3 mm long, 1.7 mm wide. Berries white.

Flowering in *Philodendron pirrense* occurs during the early rainy season, judging by post-anthesis collections from June and July.

Philodendron pirrense is endemic to Panama, where it is known for certain only from the Serranía de Pirre, at 1000 to 1560 m elevation in *Premontane rain forest.*

Philodendron pirrense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its short internodes; sharply two-high-ribbed cataphylls persisting as pale fibers with tiny fragments of thin, reddish brown epidermis; petioles somewhat flattened adaxially with a faint medial rib; broadly ovate-cordate blades with a well-developed posterior rib naked to the sinus up to half its length; inflorescences up to four per axil; and whitish peduncles clearly demarcated from the red spathe tube.

Philodendron pirrense is similar to *P. copense,* with which it shares dried leaves of similar color and persistent, reddish brown cataphylls. The latter species differs in having longer blades with the anterior lobes frequently concave along their margins and petioles with a yellowish or reddish brown flaking periderm.

Additional specimens examined. PANAMA. **Darién**: Serranía de Pirre, ca. 12 km N of Alto de Nique, 1520–1560 m, *Croat 37916* (MO); ca. 9 km from Alto de Nique, 1480–1520 m, *Croat 37887* (MO); Río Escucho Ruido, ca. 16 km N of Alto de Nique, 1530–1550 m, *Croat 37944* (MO).

Philodendron platypetiolatum Madison, Selbyana 2: 22. 1977. TYPE: Ecuador. Los Ríos: Río Palenque Science Center, km 56 on road to Santo Domingo and Quevedo, 150–220 m, ca. 0°35′S, 79°22′W, *Dodson 6638* (holotype, SEL; isotypes, MO, QCA, US). Figures 306–308.

Hemiepiphytic; stem ± scandent, loosely appressed-climbing, to 3 m long, semiglossy, sap clear, watery, sticky, leaf scars to 2 cm wide; internodes slender, 14–20 cm long, 1–2 cm diam., longer than broad, sometimes somewhat flattened on

side above, semiglossy, green to grayish green, epidermis drying tannish brown, cracking, loosening and flaking; roots pale to brownish, less than 20 cm long, thin, 2 mm diam., smooth; cataphylls (6)10–17 cm long, sharply 2-ribbed, sharply and deeply sulcate with margins flared, pale to medium green, drying yellowish to olive-green, deciduous; **petioles** 15.5–56 cm long, 3–9(12) mm diam., broadly flattened to markedly flattened and turned slightly upward adaxially, broadly convex abaxially, firm, medium to dark green, surface ± unmarked; **blades** ovate-triangular to broadly ovate, subcoriaceous, semiglossy to glossy, weakly to moderately bicolorous, acuminate, sometimes long, narrowly acuminate at apex (the acumen tightly inrolled, 2–3 mm long), weakly cordate at base, 17–39 cm long, 12.7–29 cm wide (1–1.5 times longer than wide), (0.6–1.4 times longer than petiole), usually about equal in length to petiole; anterior lobe 15–34 cm long, 13–29 cm wide (2.4–4.5(5.2–5.4) times longer than posterior lobes); posterior lobes 4–10 cm long, 5–12 cm wide, broadly rounded to obtuse; sinus hippocrepiform, rarely arcuate with blade decurrent on petiole; midrib sunken or flat to broadly convex above, slightly paler than surface to concolorous above, bluntly low-triangular to convex below, paler than surface below; basal veins (2)3–4(5) per side, with 0–1 free to base, second and third coalesced 1–2 cm; posterior rib naked for 0–1 cm; primary lateral veins 3–5 per side, departing midrib at a 50–60° angle, straight to the margins, sunken to weakly sunken above, convex below; minor veins moderately indistinct, arising from both the midrib and primary lateral veins. INFLORESCENCES 1(2) per axil; peduncle 5–20 cm long, 2–11 mm diam., subterete or bluntly 1–2-angled, pale green, semiglossy, unmarked; **spathe** semiglossy, (8)11–18 cm long (0.7–2(2.8) times longer than peduncle); spathe blade green or red outside, pale yellow-green (dark red in South America), inside; spathe tube green to olive-green, usually tinged red or maroon outside, 4.5–7.5 cm long, tinged red or maroon inside; **spadix** sessile; weakly tapered, ± acute at apex, 8–9.8 cm long, broadest at the base or ± uniform throughout, constricted weakly between sterile and fertile staminate portions; pistillate portion pale greenish, cylindrical or weakly tapered toward the apex, 2.5(3.5) cm long, 9–11 mm diam. at apex, 10–13 mm diam. at middle, 10–13 mm wide at base; staminate portion 5.7–7.3 cm long; fertile staminate portion white, weakly tapered or cylindrical, 5–7 mm diam. at base, 4–5 mm diam. ca. 1 cm from apex, broadest at the base or ± uniform, narrower than the pistillate portion, broader than or as broad as the sterile portion; sterile staminate portion as broad as or slightly narrower than the pistillate portion, 5–10 mm diam.; pistils (0.8)1.7–2.5 mm long, (0.6)0.9–1.4 mm diam., white; ovary (6)7–8-locular, (0.7)1.1–1.8 mm long, 0.8–1.2 mm diam., with sub-basal placentation; locules 0.7–1.5 mm long, 0.3 mm diam., ovule sac 0.8 mm long; ovules 3 per locule, 1-seriate, contained within translucent to transparent, gelatinous envelope, (0.2–0.3)0.4–0.5 mm long, longer than funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style (0.1)0.4–0.7 mm long, 0.6–0.8 mm diam., similar to style type B; style apex steeply sloping, sometimes with small medial depression; stigma subdiscoid to hemispheroid, somewhat cupullate, 0.7–0.9(1.3) mm diam., 0.2–0.3 mm high, covering entire style apex; the androecium prismatic, truncate, oblong, margins irregularly 4–6-sided, sometimes weakly scalloped; thecae cylindrical to oblong, 0.3–0.4 mm wide, ± parallel to one another, sometimes ± contiguous; sterile staminate flowers irregularly 4–6-sided or rounded, 0.9–1.5 mm long, 0.7–1.2 mm wide. INFRUCTESCENCE turning red outside; berries green (immature).

Flowering in *Philodendron platypetiolatum* occurs in the early rainy season, June and September, in Central America based on the few available flowering collections. Post-anthesis collections from Costa Rica and Panama are mainly from August through November, but also from March. Immature fruits have been collected only in January, February, and November. Ecuadorian populations have a similar phenology, but flowering collections have been made earlier, in March and April, with post-anthesis collections from March through August.

Philodendron platypetiolatum ranges from Nicaragua to Ecuador, from sea level to 1500 (though most collections are from below 400) m elevation, in *Premontane wet forest, Tropical wet forest* transition to *Premontane wet forest,* and *Tropical wet forest* life zones. This species has been collected at several localities in Chocó and Valle Departments; in Ecuador, it has only been collected at and near the type locality.

Philodendron platypetiolatum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium.* This species is characterized by its scandent habit; moderately long, slender internodes with tannish brown, frequently flaking epidermis; markedly flattened petioles about as long as the blade; and ovate-triangular to broadly ovate, weakly cordate blades. Though the spathes may be entirely green outside, they usually are heavily tinged with red or maroon outside and the tube within is likewise colored.

There are no other species in Cental America with which *P. platypetiolatum* might be confused. Madison compared this species to *P. lechlerianum* Schott, a species from Peru and Bolivia that has terete petioles.

In Panama, this species ranges along the Atlantic slope but may also occur on the Pacific slope near the Continental Divide. In Ecuador, it is restricted to the Pacific slope.

Ecuadorian specimens have blades that are more broadly ovate than those from Panama, but no other differences have been detected.

Additional specimens examined. COSTA RICA. **Alajuela**: Upala Road, 3 km NNE of Bijagua, 450 m, 10°45′N, 85°3′W, *Burger & Baker 9890* (CR, F, MO, NY, SEL); 5 km S of Canalete, near Río Zapote, 100–200 m, 10°48′N, 85°2′W, *Burger & Baker 9972* (F, MO); Dos Ríos, 5 km S de Brasilia, Río Pizote, 500 m, 10°55′N, 85°20′W, *Herrera 1001* (CR, MO, SAR); 17 km NW of San Ramón, 785 m, 10°14′14″N, 84°33′W, *Croat 68136* (F, MO); Bajo Rodríguez–La Tigra, vic. of La Tigra, 330 m, 10°22′N, 84°38′W, *Croat 68205* (B, CM, G, M, MO, SAR, US); Monteverde Cloud Forest Nature Reserve, Río Peñas Blancas, 1250–1350 m, 9°17′N, 84°86′W, *Burger et al. 10745* (F, MO); Vara Blanca–Puerto Viejo, 3 mi. N of San Miguel, 380 m, *Croat 35666* (MO); Cañas–Upala, 13.8 km N of Bijagua, 100–150 m, *Croat 36433* (MO); 4 km NNE of Bijagua, ca. 400 m, *Croat 36269* (MO); slopes of Miravalles, above Bijagua, *Gómez et al. 19066* (MO); Naranjo–Aguas Zarcas, along Hwy. 15, 8.5 km NE of Villa Quesada, 600 m, *Croat 46973* (CR, MO). **Heredia**: "Starkey Road," 4.5 km SE of bridge at Puerto Viejo, ca. 50 m, 10°26′N, 83°58′W, *Stevens 13489* (MO); La Selva Field Station, *Grayum 2228* (MO); 100 m, *McDowell 329* (MO); 100 m, *647* (CAS); 50–80 m, 10°26′N, 84°01′W, *Grayum 7665* (CR, MO); 6 km from Río Peje crossing, 5 km SSE of Magsasay, 340 m, 10°21′N, 84°04′W, *Schatz & Grayum 634* (CR, MO); Puerto Viejo de Sarapiquí, 100 m, *Croat 44248* (MO); 10°26′N, 84°01′W, *61213* (MO); Parque Nacional Braulio Carrillo, Río Peje–Río Sardinalito, Volcán Barva, 700–800 m, 10°17′30″N, 84°05′W, *Grayum & Herrera 7908* (CR, F, MO, VEN). **Limón**: Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson 6744* (RSA), *Davidson & Donahue 8383* (F, MO, RSA); *Davidson & Donahue 8802* (MO); *8874* (MO, RSA); Barra del Colorado, 0–2 m, 10°47′N, 83°35′W, *Stevens 24214* (CR, MO); Cerro Coronel, 20–170 m, 10°41′N, 83°38′W, *Stevens 24623* (CR, MO); Quebrada Danta, W of Guápiles, 360 m, 10°12′N, 83°49′W, *Croat 68426* (MO, NY); Braulio Carrillo–Guápiles, 250–270 m, *Croat 78744* (CR, INB, MO); Río Colorado, 14 km by air SW of Barra del Colorado, 10–120 m, 10°40′N, 83°40′W, *Davidse & Herrera 31060* (CR, MO); 16 km by air SW of Barra del Colorado, 10°39′N, 83°40′40″W, *31211* (MO). **Puntarenas**: Osa Península, Piedras Blancas, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67687* (CR, K, MO); Rincón de Osa-Esquinas, 100 m, *Pennington et al. 11386* (K); Fila Gamba, ca. 6 km from Golfito airport, <100 m, 8°41′30″N, 83°12′W, *Croat 59926* (CM, K, MO); 200–300 m, *Croat & Hannon 79290* (MO). **San José**: El General Valley, Finca Volcán Angel, *Schubert & Rogerson 769* (A, GH); Braulio Carrillo National park, 600–700 m, *Croat 78778* (CR, INB, MO). NICARAGUA. **Río San Juan**: Río Santa Cruz–Caño Santa Crucita, La Palma, 40–60 m, 11°2–4′N, 84°24–26′W, *Stevens 23496* (MO). **Zelaya**: Río Sucio, E of Bonanza, ca. 140 m, 14°01′N, 84°34′W, *Stevens 12347* (MO); Mpio. Siuna, Comarca Danlí, 100–130 m, *Ortiz 218* (MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, 9.4 mi. N of Continental Divide, 175 m, 8°46′N, 82°16′W, *Croat 66822* (AAU, MO). **Colón**: Río Guanche, ca. 3–4 km above bridge on road to Portobelo, *J. Witherspoon & F. Witherspoon 8662* (CAS, MO); Sabanitas–Portobello, Río Piedras Lumber Road, 6.7 mi. E of Sabanitas, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75166* (MO, PMA). **Darién**: Parque Nacional Cerro Pirre region, Cana, 500–600 m, *Croat 37661* (MO); near station along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77116* (MO); Parque Nacional Darién, Río Topalisa–Río Pucuro, ca. 17 km E of Pucuro, Mi Casita–La Laguna, 600–850 m, 8°03.5′N, 77°17′W, *de Nevers et al. 8337* (CAS, MO); ca. 5 km E of Pucuro, Quebrada Maskia, 200 m, 8°01′N, 77°25′W, *Hammel et al. 16167* (MO). **Panamá**: El Llano–Cartí, 13.8 km N of Pan-American Highway, *Folsom et al. 5788* (MO); Mile 6.8, 350 m, *Croat 49125* (MO, PMA); Cerro Jefe region, 0.8 mi. beyond turnoff to Altos de Pacora, 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76645* (MO); 4.6 km beyond peak on road to Altos de Pacora, ca. 600 m, *Croat 35936* (MO); near summit, 750–800 m, 9°14′N, 79°22′W, *Croat 67083* (MO); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68680* (CM, MO). **San Blas**: El Llano–Cartí Road, vic. Nusagandi, 300–350 m, 9°15′N, 79°W, *Croat 69278* (CM, MO); 450 m, 9°18′N, 79°59′W, *Croat 75118* (CAS, MO, NY, PMA); 10.1 mi. N of main highway, 300 m, 9°20′N, 79°W, *Croat & Zhu 76539* (CM, M, MO); Mile 9, 350 m, 9°20′N, 79°W, *Croat 76999* (MO); Río Playón Chico, 80–200 m, 9°13.5′N, 78°15′W, *Herrera & Arosemena 1778* (AAU, COL, CR, K, MEXU, MO, NY, P, PMA, STRI, US).

Philodendron pseudauriculatum Croat, sp. nov. TYPE: Panama. Panamá: El Llano–Cartí road, 4 mi. from Inter-American Hwy. near El Llano, ca. 300 m, 27 Mar. 1976, *Croat 33730* (holotype, MO–2381528; isotypes, PMA, RSA, SEL). Figures 35, 300, 309, 310, 313, 314.

Planta hemiepiphytica; internodia 1.4(9) cm longa, 2–4 cm diam.; cataphylla 18–27 cm longa, acute 2-costata, decidua; petiolus subspongiosus, 11–42 cm longus, 0.7–2.6 cm diam., subteres, leviter complanatus adaxialiter, late et obtuse sulcatus in medio, cum annuluo viridi apice; lamina oblongo-elliptica vel oblanceolato-elliptica, plurumque acuta vel anguste rotundata, interdum subcordata truncata basi, 27–80 cm longa, 7.5–25 cm lata; in sicco atricaniviridis; inflorescentia 2–3; pedunculus 5.5–21(25) cm longus, 8–12 mm diam.; spatha (10.6)12–23 cm longa, omnino alba vel subrosea, marginibus cremeis; lamina spathae extus eburnea vel flaviviridi, striata flaviaurantiaca, intus pallide viridi vel alba; tubo spathae extus vel atriviridi, interdum extus leniter suffuso purpurascenti secus margines, vivide rubriviolaceo vel atrimarronino vel flaviaurantiaco; pistilla 5–8(9)-locularia; loculi 1–2(4)-ovulati; baccae aurantiacae.

Hemiepiphytic; stem appressed-climbing, to 1 m long; internodes gray-green, glossy to semiglossy,

1–4(9) cm long, 2–4 cm diam., usually somewhat flattened on one side, frequently with a short series of transverse ridges just below the nodes on both sides of the rounded portion of internodes, usually about as broad as long, or broader than long on flowering plants, sometimes slightly longer than broad; roots dark brown, slender, few per node; cataphylls moderately spongy, 18–27 cm long, sharply 2-ribbed (ribs to ca. 1 cm high), medium green, densely dark green short-lineate, deciduous, apiculate (apiculum >1 cm long) at apex. LEAVES erect, ± rosulate, somewhat clustered at or near stem apex; **petioles** 11–42 cm long, 0.7–2.6 cm diam., subterete, somewhat spongy, slightly flattened, bluntly and broadly sulcate midway, less so toward apex, more so toward base adaxially, surface medium green, semiglossy, with dark green ring around apex; **blades** oblong-elliptic to oblanceolate-elliptic, subcoriaceous to coriaceous, somewhat to markedly bicolorous, semiglossy, acuminate, sometimes long-acuminate at apex, mostly acute to rounded, sometimes broadly subcordate, or sometimes truncate at base, 27–80 cm long, 7.5–25 cm wide (2.2–4(5) times longer than wide), (0.97–3.6 times longer than petiole), upper surface dark green, drying dark gray-green, lower surface much paler, yellow-green, drying yellow-green to yellow-brown; sinus (when present) to 2.5 cm deep; midrib flattened at base, slightly sulcate midway, broadly convex at apex and concolorous above, convex, short-green-lineate, paler than surface below; basal veins (0)1–3(4), all free to base; posterior rib lacking; primary lateral veins 8–14 per side, departing midrib at a 65–75° angle (45–55° angle at apex), ± straight to the margins, sunken above, convex and slightly paler than surface or darker than surface below; interprimary veins flat, darker than surface below; minor veins moderately distinct and fine below, arising from both the midrib and primary lateral veins. INFLORESCENCES 2–3 per axil; peduncle 5.5–21(25) cm long, 8–12 mm diam., pale to medium green, finely white- or dark-striate; **spathe** (10.6)12–23 cm long, 1.7 cm diam. (0.7–2.6 times longer than peduncle), constricted midway above the tube, white to pinkish throughout, margins cream; spathe blade creamy white to yellowish green with faint green tinge along center on backside (B & K yellow-red 7.5/9), yellow-orange striate outside, 8.5–9 cm long (opening elliptic in face view, 7.5–9 cm long, 2–5.5 cm wide), pale green to white inside; resin canals orange; spathe tube oblong-ellipsoid, medium to dark green, sometimes weakly tinged purplish along margins outside, densely short white-lineate, semi-glossy outside, 5.5–10.5 cm long, 1.8–4 cm diam., bright red-violet to dark maroon (weakly so toward apex) to yellowish orange, sometimes broad, white-lineate or orange striate inside; **spadix** weakly stipitate to 3–5 mm long, cylindrical to weakly tapered, 7.5–15.3 cm long, broadest below the middle; pistillate portion cylindrical to clavate, pale lime green to pale yellow to medium or dark green, 3–5.5 cm long in front, 1.7–4 cm long in back, 1–1.2 cm diam. at apex, 1.5 cm diam. at middle, 8–11 mm wide at base; staminate portion 4.5–10.7(12) cm long; fertile staminate portion broadest in middle, slightly tapered toward both ends and broadened before the sterile portion, 9–16 mm diam. at base, 9–10 mm diam. at middle, 5–10 mm diam. ca. 1 cm from apex, broadest at the base, as broad as the pistillate portion, narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, white, 8–15 mm diam.; pistils 1.7–3.2 mm long, 1.3–2 mm diam.; ovary 5–8(9)-locular, 1.4–2.3 mm long, 1.5–2 mm diam., with sub-basal placentation, walls embedded with granular, crystal-like particles; locules 1.4–2.1 mm long, 0.3–0.5 mm diam.; ovule sac 1–1.2 mm long; ovules 1–2(4) per locule, contained within transparent, gelatinous ovule sac, 0.4–0.5 mm long, longer than funicle; funicle 0.1–0.5 mm long (can be pulled free to base), style 0.4–1.4 mm long, 0.9–2.1 mm diam., similar to style type B; style apex sloping to rounded, with small medial depression; stigma brush-like, cupulate, subdiscoid, 0.9–1.2 mm diam., 0.2–0.6 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 1.3–1.4 mm long, 1.6–1.8 mm diam. at apex; thecae oblong to cylindrical, 0.4–0.5 mm wide, nearly contiguous and ± parallel to one another; pollen ellipsoidal to spheroidal, <1 mm long, <1 mm diam.; sterile staminate flowers irregularly 4–5-sided, margins bluntly rounded, 1.2–1.9 mm long, 1.8 mm wide. Berries orange (mature) or white; seeds 5 per berry, 1.3–1.9 mm long, 0.5–0.7 mm diam.

Flowering in *Philodendron pseudauriculatum* occurs during the dry season and the first half of the rainy season (January through September). Immature fruits have been collected during March, June, and July, with mature fruits known only from September.

Philodendron pseudauriculatum is definitely known only from Panama and adjacent Colombia (N Antioquia), ranging from 20 to 1400 m elevation in *Premontane wet forest* and *Tropical wet forest* life zones. Most collections have been made at La Mesa (Coclé), Cerro Campana (Panamá), and along the El Llano–Cartí Road (Panamá), but the species is

also known from a single collection in Bocas del Toro and in the Serranía de Cañasas along the Pacific Ocean.

Philodendron pseudauriculatum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. This species is recognized by its appressed-climbing habit; short internodes; more or less rosulate habit; somewhat spongy, subterete petioles; oblong-elliptic to oblanceolate-elliptic, dark gray-green-drying blades with mostly narrowly rounded bases, and two to three inflorescences per axil; and white to pinkish spathes clearly demarcated from the peduncles.

Philodendron pseudauriculatum is most easily confused with *P. ligulatum*, especially *P. ligulatum* vars. *heraclioanum* and *ligulatum*, which have similarly shaped blades. *Philodendron ligulatum* var. *heraclioanum* differs in having sharply D-shaped petioles with undulate-margined wings. While the aforementioned varieties of *P. ligulatum* differ in their usually vining habit and typically elongate internodes, these features are particularly apparent in *P. ligulatum* var. *ligulatum*, which has internodes much longer than wide (vs. about as long as broad or scarcely longer than broad as in *P. pseudauriculatum*). In addition, the leaves of *P. ligulatum* frequently dry much darker, mostly somewhat blackened, rather than the typical yellowish or brownish green of *P. pseudauriculatum*. Another feature separating live material of the species is the line of demarcation at the apex of the petiole, which is purple in *P. ligulatum* rather than green as in *P. pseudauriculatum*.

Philodendron pseudauriculatum may also be confused with both *P. auriculatum* (hence the epithet "pseudauriculatum"), from the Pacific slope of southwestern Costa Rica and *P. wendlandii* Schott from the Atlantic slope of Costa Rica and Panama. *Philodendron auriculatum* is distinguished by having leaf blades drying a paler yellow-green color and more narrowed toward the base with minute narrow auriculate posterior lobes. It also has proportionately somewhat longer petioles. *Philodendron wendlandii* differs in having a much shorter stem and petioles typically broader than thick with sharp margins.

Two collections (*Croat 16908* and *Knapp & Mallet 4658*) from San Blas at Puerto Obaldía are probably also this species. They differ in having broader blades and drying somewhat blacker. If these prove to represent *P. pseudauriculatum*, the species is most assuredly present in adjacent Chocó. A collection from the Department of Santander in Colombia at 1460 to 1700 m (*García-Barriga & Jaramillo 19671*) may also be this species.

Additional specimens examined. PANAMA. **Bocas del Toro**: Quebrada Huron, Duwebdulup Peak, N of Río Terebe, 300–900 ft., *Kirkbride & Duke 558* (MO). **Canal Area**: Summit Gardens, *Croat 10791* (F, MO, SCZ). **Coclé**: El Valle region, La Mesa, 650–710 m, *Mori et al. 1916* (MO); *Luteyn & Kennedy 1660* (DUKE); *Hammel 3844* (MO); 860–900 m, *Croat 37420* (MO); 900 m, *22964* (MO); *14362* (MO); 800 m, *Croat & Zhu 76692* (MO); *Bartlett & Lasser 16694* (F, MICH, MO); *Kennedy et al. 3189* (MO, PMA); 785 m, 8°37′N, 80°08′W, *Croat 67112* (MO); summit of Cerro Caracoral, near La Mesa, N of El Valle de Antón, 1100 m, *Knapp 1118* (K, MO); Río Cascajal, Penonomé–Coclecito, 5.6 mi. N of Llano Grande, 150 m, 8°46′N, 80°27′W, *Croat 67484* (AAU, CAS, COL, F, L, MEXU, MO, NY, PMA, QCA, TEX). **Colón**: near Peluca, on road to Nombre de Dios, *Kennedy 2774* (F, MO); Portobelo–Nombre de Dios, Nuevo Tonosí, <100 m, *Croat 33526* (CM, COL, K, L, MO, NY, PMA, QCA, RSA, US); Sabanitas–Portobelo, Río Piedras drainage, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75160* (MO); Portobelo, *Croat & Porter 15606* (MO); Río Boquerón, near No. 1 (manganese mine), E of Salamanca, 50 m, 9°35′N, 79°32′W, *Knapp et al. 5832* (B, K, MO); Puerto Pilón–Portobelo, ca. 1.5 mi. above bridge, <100 m, 9°27′N, 79°4′W, *Croat & Zhu 76251* (CR, MO, PMA); Río Guanche, 30–100 m, *Croat 79322* (PMA); ca. 5 km upstream from road to Portobelo, 50 m, 9°30′N, 79°40′W, *Hammel & Trainer 14765* (MO); ca. 3–5 km above bridge, 50–200 m, *Croat 37002* (MO); 10–100 m, *26147* (BR, F, MO); ca. 50 m, ca. 9°30′N, 79°40′W, *McPherson 8507* (MO); Río Iguanita, near bridge along Portobelo Road, <50 m, 9°27′N, 79°42′W, *Croat 49778A* (MO); Río Miguel de la Borda, vic. of Guásimo, *Croat 9985* (MO, SCZ); Río Sirrí, Trinidad Basin, 20–50 m, *Pittier 4015* (US). **Darién**: Cerro Pirre National Park, W side of Cerro Pirre, base camp, 50 m, 8°N, 77°48′W, *Croat 68962* (M, MO, NY, US); near station along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77094* (CM, MO); Cerro Pirre region, trail NW of Cana, 600 m, *Sullivan 712* (MO); Cana, near Río Setigandi, 540–580 m, *Gentry et al. 28542* (MO); Cana gold mine, vic. of airstrip, 480 m, *Croat 38038* (MO); 500–600 m, *37595* (MO), along Río Cana, SW of Cerro Pirre, 1400 m, *Croat 27292* (MO); Río Coasi, 0–2 mi. E of Tres Bocas, *Kirkbride & Duke 1203* (MO, NY); Río Cocalito, *Whitefoord & Eddy 224* (BM); *162* (BM, MO); Río Jaqué Valley, Quebrada Luka, 100–200 m, 7°27′N, 78°05′W, *Knapp & Mallet 3199* (MO, NY); Río Tuquesa, ca. 2 km by air from Continental Divide, *Croat 27160* (F, MO); *Clezio 168* (MO). **Panamá**: El Llano–Cartí Road, 5 mi. from Pan-American Highway, 350 m, *Croat 67345* (CAS, MO); Km 8–12, ca. 400–450 m, *Nee et al. 8802* (MO); ca. Mile 8, 225–275 m, 9°15′04″N, 79°00′04″W, *McPherson 10492* (AAU, MEXU, MO); Km 19.1, 350 m, 9°19′N, 78°55′W, *de Nevers et al. 7342* (MO); Río Terabe Valley, El Llano–Cartí, 8 km from highway, 300–400 m, 9°16′N, 79°W, *Knapp & Schmalzel 5493* (MO); area around Pilota de Toro, *Folsom et al. 6819* (MO, PMA); Tortí–Pilota del Toro, above Tortí Arriba, *Folsom et al. 4993* (MO, PMA); Cerro Campana, 6.1 mi. above Pan-American Highway, 800 m, 8°41′N, 79°56′W, *Croat 74762* (F, MO); ca. 1 mi. from highway, ca. 150 m, *35991* (MO); along trail to summit, 780–875 m, *25253* (MO, NY, PMA, US); ca. 850 m, 8°42′N, 79°56′W, *Miller et al. 754* (MO); upper slopes, 207 m, *LeDoux 2595* (MO); above Su Lin Motel, *Porter et al. 4250* (MO); Río Tortí, base of Serranía de Cañazas, ca. 15 km SW of Caaza, 150 m, 8°52′N, 78°22′W, *Stein 1342* (MO); Sendero de Interpre-

tación, 1 km al este del Campamento de los guardabosques de INRENARE, 800–900 m, 8°40′N, 79°55′W, *Correa & Montenegro 10681b* (STRI). **San Blas**: El Llano-Cartí Road, Km 19, 350 m, 9°19′N, 78°55′W, *de Nevers et al. 5598* (MO); Puerto Obaldía, 0–50 m, *Pittier 4398* (US); beach E of Puerto Obaldía, *Croat 16908* (MO); Puerto Obaldía–La Bonga, ca. 2 hours walk from Puerto Obaldía, 0–50 m, 8°40′N, 77°25′W, *Knapp & Mallet 4658* (MO); Nusagandi, El Llano–Cartí Road, 10.1 mi. N of main highway, 300 m, 9°20′N, 79°W, *Croat & Zhu 76554* (CM, MO); Río Playón Chico, 80–200 m, 9°13′05″N, 78°15′W, *Herrera & Arosemena 1784* (MO, PMA, STRI).

COLOMBIA. **Antioquia**: Mpio. Turbo, carretera tapón del Darién, sector Río León–lomas aisladas, km 37, 20 m, *Brand 1070* (COL, MO). **Chocó**: Mecana, N of Bahía Solano, 1–100 m, 6°16′N, 77°21′W, *Juncosa 1609* (MO). **Risaralda**: Mistrató, Jeguadas–Santa Cecilia, 800–850 m, 5°24′N, 76°01′W, *Betancur et al. 3459* (MO); corregimiento de Santa Cecilia, 500–550 m, 5°17′N, 76°13′W, *Betancur et al. 2930* (MO); Pueblo Rico, Santa Cecilia–Pueblo Rico, Km 13, Quebrada Pionda, 700–900 m, 5°17′N, 76°13′W, *Betancur et al. 3052* (MO).

Philodendron pterotum K. Koch & Augustin, in A. Braun et al., Append. gen. sp. Hort. berol. 1854: 6. 1854–1855. TYPE: Cultivated at Berlin [received from Warszewicz in Venezuela] (holotype, B? lost). Panama. Canal Area: vic. Fort Sherman, along road between Gatún Locks and Fort Sherman, ca. 3 mi. W of Gatún Locks, <50 m, 9°19′N, 79°57′30″W, 17 July 1994, *Croat & Zhu 76982* (neotype, MO–4619421–26, here designated; isoneotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, GB, GH, K, MEXU, P, PMA, QCA, RSA, SEL, VEN, W). Figures 311, 312, 315, 316.

Philodendron mirificum Standl. & L. O. Williams, Ceiba 3: 38. 1952. TYPE: Costa Rica. Puntarenas: near Palmar Sur de Osa, 75 m, 24 Mar. 1951, *Allen 6031* (holotype, EAP; isotype, F).

Usually hemiepiphytic or epiphytic; stem appressed-climbing, semiglossy, sap watery, weakly turpentine-scented, leaf scars conspicuous, 2 cm long, 1 cm wide; internodes sometimes obscured by cataphylls, sparsely short-striate, about as long as broad or sometimes longer than broad, 2–8 cm diam., dark green to gray-green, eventually brown, epidermis sometimes cracking, fissured longitudinally; roots short, few per node; cataphylls 20–30 cm long, sharply 2-ribbed, C-shaped, semiglossy, dark green, densely pale lineate, persisting as reddish brown, semi-intact fibers, eventually deciduous; **petioles** (37)47–111 cm long, (3–5)6–13(16–22) mm diam., erect-spreading, D-shaped, marginally winged, broadly convex adaxially, with adaxial margins slender, erect, undulate, medium green, weakly glossy, conspicuously pale striate; sheath with margins involute; **blades** ovate, subcoriaceous, semiglossy, moderately bicolorous, abruptly acuminate at apex (the acumen inrolled, 2–4(6) mm long), broadly cordate at base, 36–93 cm long, 22–84 cm wide (0.7–1.5(2.9) times longer than wide), (0.6–0.9 times the petiole length), margins weakly undulate, upper surface dark green, lower surface much paler, glossy, drying yellow-green; anterior lobe 23.5–65(84) cm long, 22.1–75(86.4) cm wide (1.1–2.8 times longer than posterior lobes); posterior lobes 12–33 cm long, (11)15–34 cm wide, directed inward, broadly rounded to broadly obtuse; sinus spathulate to rhombic; basal veins 7–10 per side, first free to base, part of remainder coalesced 1–6 cm, loosely so distally; posterior rib naked to 6 cm; midrib flat to broadly sunken, paler than surface above, convex to narrowly rounded, paler than surface below; primary lateral veins 3–6 per side, departing midrib at a 45–55° angle, ± straight to weakly arcuate to the margins, deeply sunken, paler than surface above, raised to convex, paler than surface below; interprimary veins weakly raised, darker than surface below; the minor veins moderately distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2–4 per axil; peduncle (2)4–12 cm long, 4–13 mm diam., medium green, coarsely white streaked toward apex; **spathe** 11–29 cm long (1.4–3.8(5) times longer than peduncle), ± cuspidate at apex; spathe blade light green outside, greenish white inside; spathe tube abruptly delineated from tube, reddish to purplish to dark purple-violet (B & K purple 2/10) or dark green and raised-white-striate at base outside, red to magenta inside; **spadix** weakly stipitate, exserted from the spathe, constricted above sterile staminate portion; pistillate portion pale green, 4.3 cm long in front, 3.8 cm long in back, 2 cm diam. at apex, 1.7 cm wide at base; staminate portion 16–18 cm long; fertile staminate portion white, 1.7 cm diam. at middle; sterile staminate portion 1.4–2.2 cm diam.; pistils 2.2–2.8 mm long, 1.1–1.4 mm diam.; ovary 6-locular, with axile placentation; locules 1.5–1.9 mm long, 0.4 mm diam.; ovules ca. 20 per locule, 2-seriate, somewhat translucent, 0.2–0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition, style similar to style type B; style apex flat to weakly rounded; stigma subdiscoid to weakly hemispheroid, sometimes weakly lobed, 1.5 mm diam., 0.5 mm high, covering entire style apex; the androecium truncate, prismatic, margins irregularly 4–6-sided, 0.7–1.5 mm long; thecae oblong, 0.4 mm wide, not contiguous, ± parallel to one another; sterile staminate flowers irregularly 4–5-sided, 1.5–2.5 mm long. INFRUCTESCENCE with spathe green at base and tip, pur-

ple around fruiting area when ripe, berries pale brown to white. JUVENILE and PRE-ADULT plants with petioles flattened adaxially; blades broadly ovate. PRE-ADULT blades broadly ovate, 28.5 cm long, 22.5 cm wide.

Flowering in *Philodendron pterotum* occurs in the early rainy season from May through August based on both specimens and field observations; it certainly must flower during part of the dry season as well, since post-anthesis collections have been made as early as March. Other post-anthesis collections have been made in April and May but especially in June. Immature fruits have been collected in February, March, May, July, October, and November, especially October. Mature fruits have been collected only in November.

Philodendron pterotum ranges from Nicaragua to Central Panama, from sea level to 1900 (mostly below 700) m elevation in *Tropical moist forest* and *Tropical wet forest* life zones. In Nicaragua it occurs only on the Atlantic slope, but in Costa Rica and Panama it occurs on both slopes.

Philodendron pterotum is a member of *P.* sect. *Philodendron* subsect. *Platypodium*. This species is characterized by its broadly ovate juvenile leaves with flattened petioles; appressed-climbing adult habit with short internodes; persistent cataphyll fibers; D-shaped petioles with slender, erect, undulate, marginal wings; and large, ovate, yellow-green-drying blades with large inflorescences with the spathe tube reddish to purplish on the outside and much darker magenta within.

No type material has survived for *P. pterotum*. The species was described from cultivated material of a juvenile plant purportedly received from the "little garden of Cl. Augustin," which the tireless traveler (Mr. Augustin) collected from Warszewicz in Venezuela. It is important to note that it was not said to have been collected in Venezuela (where it does not occur), but only that it was obtained from Warszewicz in Venezuela. There is much uncertainty involved, since the extrapolation of juvenile forms to adult plants is at best risky, even at the type locality. Given the frequency of mishaps involving the dispersal of living material among horticulturists and botanical gardens, there is always the chance of a mislabeled plant.

Still, while it is not possible to confirm the true nature of Koch and Augustin's plant, it is certain that the plant which Schott illustrated in detail (Icones #2478, #2480, #725, and #726) really does represent the plant currently being called *P. pterotum*. Although this Central American species does not occur in Venezuela, Koch and Augustin seemed not to state that the plant received from Venezuela had been collected there, only that it had been received from Warscewicz in Venezuela.

Krause (1913), in his revision of *Philodendron*, cited only a Wendland collection from Costa Rica. That collection is neither at Göttingen (GOET) nor Berlin (B) and must be lost. Since Engler reported the Wendland collection to be alive at the Berlin Botanical Garden and since Wendland made much of his material available to Schott, it might have been that it was the Wendland material from Costa Rica that Schott illustrated, rather than the Koch material received from Venezuela.

Whether these two elements corresponded to the same species is conjectural, but Schott would have conceivably had the opportunity to compare both, and it is reasonable to assume that he made the correct interpretation and that his use of *P. pterotum* for the Central American species is correct. In any event, there is a need for a neotype since no specimen actually seen by Koch, Schott, or Engler and Krause still exists. Therefore, a modern collection has been chosen here.

Philodendron pterotum may be confused with *P. findens*, but that species differs in having blades that dry usually blackened and promptly split pinnately into segments.

Additional specimens examined. COSTA RICA. **Alajuela**: Cañas–Upala, 13.8 km N of Bijagua, 100–150 m, *Croat 36448* (MO); Llanura de San Carlos, 18–22 km N of Aguas Zarcas, 60 m, 10°31′N, 84°24′W, *Burger & Stolze 5186* (CR, F, US). **Heredia**: La Selva Field Station, *Grayum 2064* (MO); *Hammel 8150* (MO). **Puntarenas**: Golfito, 90 m, 8°39′N, 83°11′W, *Croat 67613* (MO, US); N of Palmar Norte, trail to Jalisco, 50–700 m, *Croat 35170* (MO); Palmar Norte–Panamanian border, 110 m, *Croat 79197* (CR, INB, MO); San Vito de Coto Brus–Neily, Fila de Cal and Cuesta Fila de Cal, 300–600 m, 8°41′N, 82°56.5″W, *Hammel 14161* (MO); Carara Reserve, Quebrada Bonita, ca. 35–80 m, 9°47′N, 84°36′W, *Grayum et al. 5721* (CR, MO); Isla del Caño, 40 km NW of Corcovado National Park, *Gómez 19963* (MO); Corcovado National Park, 0–39 m, 8°42′N, 83°52′W, *Janzen 11546* (MO); *11600* (MO); 0–200 m, 8°29′N, 83°36′W, *Liesner 2850* (CR, MO); 1–10 m, *Kernan & Phillips 1026* (CR, MO); Osa Península, ca. 5 km W of Rincón de Osa, 50–200 m, 8°42′N, 83°31′W, *Burger & Gentry 8867* (CR, F, MO, NY); Quebrada Aguabuena–Quebrada Banegas, ca. 5 km W of Rincón de Osa, 300–400 m, 8°42′N, 83°33′W, *Grayum 4066* (CR, MO); vic. Boscosa, *Croat & Hannon 79245* (INB, MO); Río Claro, along Inter-American Highway, 30 m, *Croat 32945* (MO). **San José**: San Isidro del General–Dominical, 9 mi. SW of Río Pacuar, 680 m, *Croat 35372* (MO); Puriscal, Z.P. La Cangreja, 800 m, *Morales 2031* (CR). NICARAGUA. **Zelaya**: Siuna–Matagalpa, ca. 12.9 km before Caño Piedra del Balsamo, <200 m, *Stevens 8812* (MO); near Bil Tingnia, 6 km NW of Bonanza, 150 m, *Neill 3995* (MO); Cerro Baká, ca. 6.5 km E of Río Coperna, 200–300 m, 13°40′N, 84°30′W, *Pipoly 4927* (MO); *4844* (MO); Cerro Waylawás, ca.

100–200 m, ca. 13°38–39′N, 84°48–49′W, *Pipoly 4201* (MO); Siuna–Empalme, Caño Calcamo, ca. 5 km al SE de Siuna, ca. 13°40′N, 84°45′W, *Grijalva & Burgos 1536* (MO); El Empalme–Limbaika, ca. 65 m, ca. 13°39′N, 84°24′W, *Stevens 12902* (MO); Cerro Livico, 7 km NE of Siuna, 500 m, *Neill 3633* (MO). PANAMA. Bahía Soldado, *Cowell 224* (NY). **Canal Area**: Gatún–Piña, ca. 3 km S of Piña, ca. 50 m, *Croat 36929* (MO); Gatún Lake, *Hutchison & Wright 2885* (BH, UC, US); Barro Colorado Island, *Elmore X20* (F, RSA); *Fairchild 3081* (US); *Croat 10903* (MO); *10265* (MO, SCZ); *7143* (MO); *6640* (MO, PMA); *6581* (MO, SCZ); *5136* (MO); *Bailey & Bailey 328* (BH); along road between Gatún Locks and Fort Sherman, ca. 3 mi. W of Gatún Locks, 1.4 mi. E of Ft. Sherman, 9°18′N, 79°38′W, *Croat 69860* (CM, MO); Summit Gardens, *Croat 10792* (MO, SCZ). **Chiriquí**: Puerto Armuelles–San Bartolo Límite, 7 mi. W of Puerto Armuelles, ca. 120 m, *Croat 35044* (MO); 1.6 m W of Puerto Armuelles, ca. 50 m, *Croat 21933* (MO). **Colón**: 4 km E of Buena Vista, Quebrada Ancha, 80 m, *Nee 7781* (MO, US); Portobelo–Nombre de Dios, 1.2 mi. beyond the junction of the road to Isla Grande, 79°35′W, 9°40′N, *Croat 49810* (MO); Santa Rita Ridge Road, 6.5 mi. E of Boyd–Roosevelt Highway, 370 m, 9°21′15″W, 79°44′W, *Croat & Zhu 76965* (MO). **Panamá**: 26.8 km E of Bayano bridge, *Folsom 3529* (MO).

Philodendron purpureoviride Engl., Bot. Jahrb. Syst. 26: 526. 1899. TYPE: Ecuador. Guayas: Balao, *Eggers 14710* (holotype, B). Figures 317–320.

Hemiepiphytic; stem appressed-climbing, scandent, often pendent, green becoming brownish to gray-green; internodes glossy, to 25 cm long, (0.8)1–2 cm diam., longer than broad, gray-green, semiglossy, ± terete, epidermis drying light yellow-brown, conspicuously fissured or ridged but smooth, frequently flaking free; roots thin, ± twisting or sinuous, few per node; cataphylls 10–29 cm long, unribbed to obtusely 1-ribbed or bluntly to sharply 2-ribbed, cream to medium green, magenta speckled, quickly deciduous, fragile; **petioles** 9–24 cm long, 8–10 mm diam., ± terete, somewhat spongy, somewhat flattened adaxially, surface semiglossy to glossy, frequently fissured, medium green, sometimes maroon-spotted; **blades** narrowly ovate-cordate, subcoriaceous, concolorous or weakly bicolorous, acuminate to long-acuminate at apex (the acumen inrolled), cordate at base, 12–23(27) cm long, 7.4–19 cm wide (1.3–1.8 times longer than wide), (0.8–2.2 times longer than petiole), broadest just below point of petiole attachment, upper surface drying yellow-green, semiglossy, lower surface glossy; anterior lobe 10–21 cm long, 7.4–19 cm wide (2.5–4.2 times longer than posterior lobes); posterior lobes (2.8)3.6–7(8.2) cm long, (3.1)4.3–7.7 cm wide; sinus hippocrepiform; midrib convex to broadly convex and slightly paler above, convex to broadly convex and paler below; basal veins ca. 3 per side, with 0–1 free to base, 2–3 coalesced to 5 mm long, flattened to raised; posterior rib 0.5–1 cm long, never naked; primary lateral veins about 3(4) per side, departing midrib at a 55–65° angle, ± straight to the margins, convex to weakly raised above, convex below; interprimary veins drying darker than surface below; tertiary veins ± obscure to visible and darker than surface below; minor veins fine below, arising from both the midrib and primary lateral veins; "cross-veins" conspicuous (in Central America). INFLORESCENCES erect, 1 per axil; peduncle (3.5)5–7(11.5) cm long, 5–7 mm diam., subterete, purplish tinged, whitish streaked; **spathe** 11–15 cm long (1.2–3(4.3–4.7) times longer than peduncle), constricted only slightly midway above the tube; spathe blade green to greenish white, with reddish speckling outside, 7–7.5 cm long, pale greenish cream inside; spathe tube violet-purple, short-lineate outside, 6.7–7 cm long, dark violet-purple inside; **spadix** sessile; ca. 13 cm long; pistillate portion white to pale greenish white, 4.5–5 cm long, 1.5 cm diam. throughout; staminate portion 8.5–9.2 cm long; fertile staminate portion white, drying reddish brown, 1.2 cm diam. throughout; sterile staminate portion 1.5 cm diam.; pistils 7.5 mm long, 1.6 mm diam.; ovary 4–5-locular, 6.2 mm long, 1.6 mm diam., with axile placentation; locules ca. 6.2 mm long; ovules 15–25 per locule, 0.2–0.25 mm long, 2–3-seriate, style similar to style type D; style apex with low style boss. INFRUCTESCENCE with pistillate spadix 6.5–7.5 cm long, 2.5–3.5 cm wide; berries 5.9 cm long, 2.5 cm diam.; seeds 24–25 per locule, yellow-orange, 1.2 mm long, 0.5 mm diam., thin and faintly striate.

Flowering in *Philodendron purpureoviride* is apparently aseasonal with post-anthesis material collected virtually year-round. Post-anthesis or early fruiting collections have been made in every month except September, but mature fruits have been collected only in January and August.

Philodendron purpureoviride ranges from Costa Rica and Panama to the Pacific slope of Colombia and Ecuador (to Los Ríos and Guayas Provinces) from sea level to 1600 m elevation in *Premontane rain forest, Tropical wet forest, Tropical wet forest* transition to *Premontane wet forest*, and *Premontane wet forest*. In Central America, it is known primarily from the Pacific slope of Costa Rica and adjacent Panama, but also from the Atlantic slope in both countries.

Philodendron purpureoviride is a member of *P.* sect. *Philodendron* subsect. *Solenosterigma*. This species is reportedly the dominant climber in west-

ern Ecuador in forests around San Sebastián, south of Jipijapa in the province of Manabí (A. Gentry, pers. comm.).

Philodendron purpureoviride is recognized by its scandent habit; stems with the epidermis drying yellow-brown, conspicuously exfoliating and frequently fissured; terete to somewhat flattened petioles about four-fifths as long as the blades; narrowly ovate-cordate blades drying yellow-green; solitary inflorescences, with the spathe tube violet-purple on both surfaces.

Philodendron purpureoviride is closest to and perhaps inseparable from *P. lechlerianum* Schott from Peru. The latter species is known from the type collected at "San Gaván" (San Gabon) in the Department of Puno, Carabaya Province, as well as a more recent collection (*D. N. Smith 6386*) from Pasco Department. *Philodendron lechlerianum* differs in having more conspicuous and prominent cross-veins. If these names prove to be synonymous, *P. lechlerianum* is older and would extend the range of the species into the Amazon basin.

Among sympatric species, *Philodendron purpureoviride* is most easily confused with *P. hederaceum*, also a vine with ovate-cordate, greenish-drying blades. The latter species is distinguished by having stems usually drying green or dark brown and without a peeling epidermis. In addition, the blades are more coriaceous, typically more broadly ovate with more (four to six) pairs of basal veins (vs. two to three pairs for *P. purpureoviride*), and generally have more prominent primary lateral veins. *Philodendron purpureoviride* may also be confused with some sterile specimens of *P. wilburii*. The latter species has much longer peduncles and stems drying darker brown and more closely fissured with the epidermis seldom exfoliating.

Central American material of *P. purpureoviride* differs from the Ecuadorian type by having conspicuous "cross-veins" throughout most of the blade. The Ecuadorian material, by contrast, has less conspicuous minor veins which lack "cross-veins" except at or near the margins. In addition, Engler's description of the inflorescence was based solely on Eggers's field label. Since the holotype is sterile and no fertile material associated with Eggers's original collection is apparently extant, further studies should investigate whether these specimens all represent the same species.

Additional specimens examined. COSTA RICA. **Alajuela**: 3.5 km W of Fortuna, 2.5 km NW of New Volcán Arenal, 1500 m, 10°28′N, 84°41′W, *Taylor & Taylor 11706* (MO, NY, US); Cañas–Upala, 4 km NNE of Bijagua, 400 m, *Croat 36267* (MO); Upala, 600 m, *Rivera 1559* (INB, MO). **Cartago**: 12 km S of Turrialba by air, 4 km SE of Pejibaye along Río Gato, 700 m, 9°48′N, 83°42′W, *Liesner 14355* (CR, MO); Río Reventazón, Turrialba, 500–600 m, 9°53.5′N, 83°38.5′W, *Grayum & Schatz 5242* (CR, MO); Tucurrique, Las Vueltas, 635–700 m, *Tonduz 13312* (US). **Limón**: Turrialba–Limón, along Highway 32, ca. 11 mi. S of Siquirres, 650 m, *Croat 43332* (MO); Río Telire, Bajo Telire, 400–600 m, *Gómez 24119* (MO). **Puntarenas**: Zona Protectora Las Tablas, Parque International La Amistad, Finca Cafrosa, 1600–1800 m, 8°53′20″N, 82°50′30″W, *Mora 139* (CR, MO); 1680 m, *Alfaro & Navarro 29* (INB); Cerro Anguciana, 950–1150 m, 8°49′18″N, 83°11′15″W, *Grayum 10647* (CR, MO); Palmar Norte to Jalisco, 780–960 m, 8°59.5′N, 83°28′W, *Grayum 9141* (CR, F, K, MO, US); 50–700 m, *Croat 35203* (MO); Las Cruces–Neily, Fila de Cal, 1000–1400 m, *Gómez 19635* (MO, US); Cantón Golfito, 100–500 m, *Morales et al. 1903* (CR, INB); 9 km W of La Palma, along Río Rincón, *Grant & Rundell 92-02203* (CR, MO); Golfo Dulce area, Cantón de Osa, vic. of Esquinas Experiment Station, 0 m, *Allen 5370* (MO, UC, US); W of Rincón de Osa, 250–540 m, 8°42′N, 83°31′W, *Croat & Grayum 59857* (CAS, CM, CR, MO, NY); Villa Briceño–Golfito, Fila Gamba, ca. 6 km from Golfito airport, <100 m, 8°41′30″N, 83°12′W, *Croat 59902* (CR, MO); Parque Nacional Corcovado, Dos Brazos de Rio Tigre, Jiménez, along Río Madrigal, 600 m, 8°29′50″N, 83°28′55″W, *G. Herrera 4728* (CR, MO). **San José**: San Isidro del General–Dominical, 9 mi. SW of Río Pacuar, 680 m, *Croat 35348* (MO); Carara Reserve, W Montañas Jamaica, ca. 3 km NE of Bijagual de Turrubares, 500–600 m, 9°45′30″N, 84°33′W, *Grayum et al. 5851* (CR, F, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, near road to Chiriquí Grande, 650 m, 8°45′N, 82°15′W, *McPherson 9925* (MO). **Chiriquí**: Burica Peninsula, 11 mi. W of Puerto Armuelles, vic. of San Bartolo Límite, 100–500 m, *Liesner 84* (F, MO, US); 450 m, *Busey 595* (F, MO); "Ojo de Agua," Finca Hartmann, vicinity of Santa Clara (between Volcán and Río Sereno), 1520–1750 m, 8°50′N, 82°45′W, *Croat 66290* (MO, PMA, US); ca. 13 km from Río Sereno, *McPherson & Richardson 15968* (B, K, MEXU, MO, PMA, US). **Coclé**: El Valle region, La Mesa, above El Valle de Antón, 860–900 m, *Croat 37421* (MO); Finca Macarenita, 800 m, 8°36′N, 80°07′W, *Croat & Zhu 76677* (MO). **Darién**: Cerro Pirre region, Cana, 500–600 m, *Croat 37631* (MO); W slope along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77117* (MO). **Veraguas**: Santa Fe area, between Santa Fe and Calovébora, 1.7 mi. past Alto Piedra School, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76865* (MO).

Philodendron purulhense Croat, sp. nov. TYPE: Guatemala. Alta Verapaz: El Progreso–Cobán, on Hwy. CA-14, 2–3 mi. S of Purulhá, 1500–1720 m, 15°13′S, 90°12′W, 21 July 1977, *Croat 41752* (holotype, MO–2582045; isotype, GUAT). Figures 321–323, 325, 326.

Planta hemiepiphytica aut raro terrestris; internodia brevia, usque 6 cm diam.; cataphylla 20–30 cm longa, 2-costata, acute D-formata, persistentia semi-intacta; petiolus subteres, aliquantum spongeosus, obtuse complanatus adaxialiter, 32–52 cm longus, 1.5–2 cm diam.; lamina ovata vel ovato-cordata, 25–48 cm longa, 18.5–40 cm lata, in sicco atribrunnea vel nigrescens; nervis basalibus liberis ad basim; inflorescentia 1; pedunculus 2.5–7 cm longus; spatha 10–17 cm longa; lamina spathae extus vir-

idi, breve lineata; intus viridi; pistilla 6–7-locularia; loculi 13–20-ovulati.

Hemiepiphytic or rarely terrestrial, growing 3–6 m high in trees; stem appressed-climbing or creeping; internodes short, semiglossy, to 6 cm diam., broader than long, dark green, epidermis intact; roots moderately dense, drying dark brown, ca. 3 mm diam.; cataphylls 20–30 cm long, 2-ribbed, sharply D-shaped, persisting semi-intact with brownish fibers at upper nodes; **petioles** 32–52 cm long, 1.5–2 cm diam., subterete, somewhat spongy, obtusely flattened adaxially, surface semiglossy, short-lineate, usually drying brown to blackened; **blades** ovate to ovate-cordate, subcoriaceous, slightly bicolorous, acute to acuminate at apex, cordate at base, 25–48 cm long, 18.5–40 cm wide (1.2–1.97 times longer than wide), (0.6–0.98 times the petiole length), about equal in length to petiole, upper surface somewhat silvery, semiglossy, lower surface drying dark brown to blackish; anterior lobe 20–38 cm long, 18.7–38 cm wide (2.1–3.1(3.6) times longer than posterior lobes); posterior lobes rounded, 7–17 cm long, 8–17 cm wide; sinus usually hippocrepiform, 12 cm deep; midrib flat, slightly paler than surface above, convex, paler than surface below; basal veins 4–7(8) per side, with all free to base, third and higher order veins coalesced 1.5–4 cm long; posterior rib naked for 1.5 cm; primary lateral veins 3–6 per side, departing midrib at a 35–40° angle, ± straight to the margins, sunken above, convex and paler than surface below; minor veins moderately distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 2.5–7 cm long, 8–10 mm diam., whitish streaked; **spathe** 10–17 cm long (2.4–3.4(4) times longer than peduncle), constricted slightly above the tube, ± ellipsoid; spathe green, short-lineate outside, reddish purple throughout inside; spathe tube 5 cm long; **spadix** sessile; 10–13 cm long; pistillate portion 4–4.5 cm long, 1.7–2.3 cm diam. at base, 2–2.7 cm diam. midway, 1.7–1.9 cm diam. near apex; staminate portion 8–8.5 cm long; fertile staminate portion 1.8–2 cm diam., sterile staminate portion usually much broader than pistillate portion at anthesis, weakly tapered toward apex, scarcely or not at all constricted above the sterile portion, 1.4–1.8 cm diam. midway, 11–12 mm diam. 1 cm from apex, bluntly acute at apex; sterile staminate portion not very obvious, ca. 1.3 cm long, abruptly contracted at base, as broad as or narrower than the pistillate portion; pistils 6.2 mm long, 3.4 mm diam.; ovary 6–7-locular, 5 mm long, 3 mm diam., with axile placentation; locules 5 mm long, 1 mm diam.; ovules 13–20 per locule, somewhat transparent, 1 mm long, much longer than funicle; funicle 0.2 mm long, adnate to lower part of partition, style 1 mm long, 3 mm diam., similar to style type D; style apex ± rounded; style boss broad, pronounced; stigma 1–1.1 mm diam.; the androecium truncate, oblong, prismatic, margins irregularly 4–5-sided, 1 mm long, 2–2.5 mm diam. at apex. INFRUCTESCENCE with pistillate spadix 4.5–5 cm long, 3–4 cm diam.; berries 1 cm long, 4 mm diam.; seeds 6–8 per locule, oblong-ellipsoid, 2.2–2.5 mm long, 0.7–0.9 mm diam., sticky.

The flowering phenology in *Philodendron purulhense* is poorly known. No flowering collections have been made, and only one post-anthesis collection is known (July), but immature fruiting collections are known from March, July, September, October, and November. This might suggest that the species flowers throughout at least a substantial part of the rainy season and perhaps also in the dry season (December through April).

Philodendron purulhense ranges from southern Mexico (Chiapas) to Guatemala (Alta Verapaz) and Honduras (Cortés and Olancho), at 1360 to 1870 m elevation in *Tropical Lower Montane wet forest* and *Premontane wet forest* life zones.

Philodendron purulhense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is characterized by its short internodes; sharply D-shaped to two-ribbed cataphylls persisting semi-intact; subterete petioles (about as long as the blades), dark brown to blackish-drying; ovate-cordate blades with basal veins free or weakly coalesced and scarcely or not at all naked on the usually hippocrepiform sinus; solitary, short-pedunculate inflorescence, more or less elliptic green spathe; and ovaries with 13–20 ovules per locule.

Philodendron purulhense may be confused with *P. advena* because leaves of the latter species dry a similar color. *Philodendron advena* differs in having long internodes, deciduous cataphylls, more or less sagittate blades, and one to three (four) ovules per locule.

Additional specimens examined. GUATEMALA. **Alta Verapaz**: Tactic, Río Frío, 1400–1500 m, *Standley 90510* (F); Tactic–Tamahú, 1500–1600 m, *Standley 90820* (F); Río Carchá, Cobán–San Pedro Carchá, ca. 1360 m, *Standley 89902* (F). **Baja Verapaz**: Highway CA-14 to Cobán, *Croat 41189* (MO); Biotopo del Quetzal, WNW of Purulhá, 1500–1600 m, *Stevens et al. 25446* (MO); Mpio. Purulhá, El Progreso–Cobán, 1620–1720 m, 15°13′N, 90°12′W, *Croat & Hannon 63765* (CAS, CM, K, L, MEXU, MO, US, USCG). HONDURAS. **Cortés**: Parque Nacional Cusuco, Río de Cusuco, ca. 22 km W of San Pedro Sula, 1500 m, 15°30′N, 88°13′W, *Evans 1490* (EAP, MO). **Ocotepeque**: Cordillera de Celaque, 3 mi. N of Belén Gualcho,

1870 m, 14°30′06″N, 88°48′02″W, *Davidse et al. 35340* (MO). MEXICO. **Chiapas**: Mpio. Jitotol, 5 km SE of Jitotol, along road to Bochil, 1600 m, *Breedlove & Davidse 55077* (MO); Mpio. La Trinitaria, 4 km E of Laguna, near Dos Lagos, 1300 m, *Breedlove 38810* (CAS); Mpio. Las Margaritas, 12 km E of Tziscao, 1200–1300 m, *Davidse et al. 29865* (MO).

Philodendron radiatum Schott, Oesterr. Bot. Wochenbl. 3: 378. 1853. TYPE: Mexico (holotype lost). Schott ic. 2623 (neotype, here designated). Figures 1, 324, 331–335.

Epiphytic or hemiepiphytic, rarely terrestrial; stem appressed-climbing, creeping if terrestrial, sap clear to orange, watery, sticky, leaf scars conspicuous, 2–4(7.5) cm long, 2.5–6(7) cm wide; internodes thick, 3–7(12) cm long, (1)3–8 cm diam., about as long as broad or longer than broad, dark green to gray-green, sometimes scurfy and light brownish tan, transverally lined (raised 2 mm); roots 4 mm diam., with swollen nodes and branched tips; cataphylls to 38 cm long, soft, bluntly to sharply 2-ribbed, rarely unribbed, green, sometimes conspicuously reddish-lineate, deciduous; **petioles** 28–108 cm long, (2–3)4–17 mm diam., terete or subterete to obtusely flattened adaxially, dark green, surface dark greenish or to greenish red-lineate; sheath persisting, sometimes moderately spongy; **blades** ± triangular-ovate in outline, (15)27–101 cm long, (11)25–90 cm wide (ca. 0.8–2.1 times longer than wide), (0.5–1.7 times longer than petiole), broadest at point of petiole attachment, thinly coriaceous, weakly to moderately bicolorous, semiglossy, acuminate to long-acuminate at apex, upper surface dark green, lower surface slightly paler, usually drying yellow-brown to reddish brown on both surfaces; margins weakly incised-lobate to usually deeply incised-lobate to within 1–8 cm of midrib, rarely entire and sagittate; apex often acute, sometimes acuminate, very short acuminate or ± rounded (the acumen tightly inrolled if present, 1–8 mm long), lobed-cordate at base; basal segments pinnatifid, lateral segments entire, sinuate or the lowermost of the anterior lobe pinnately lobed with 1–2 lobes on each side, final divisions linear-lanceolate in shape (0.9–2.1 times longer than wide), segment apex obtuse to broadly obtuse; interlobal sinuses 0.7–0.97 the length of the lobes; basal sinus hippocrepiform to obovate or closed, 3–15 cm deep; midrib slightly raised to convex, weakly reddish green-lineate, concolorous to paler than surface above, convex to prominently raised to round-raised below; basal veins 4–5(8) per side, directed into the segments of the posterior lobe, 0–1 free to base, (1)2–4 coalesced to 3 cm long, naked 1–6 cm; posterior rib absent; primary lateral veins 3–8 per side, departing midrib at a 50–60° angle, straight to margin, weakly raised above, raised to convex and paler than surface below; minor veins moderately visible, paler and slightly raised below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 1–3(4) per axil; peduncle 2–12 cm long, (3)5–10(19) mm diam.; **spathe** erect, 11–25 cm long (1.3–6.3 times longer than peduncle), obscurely striate, margins paler; spathe blade cuspidate at apex, pale green to yellowish green, semiglossy, sparsely purplish-dotted outside, pink to dull red or pale brownish (post-anthesis) inside; spathe tube dark purple-violet or dark green, sometimes tinged purple-violet outside, 4 cm diam., dark purple-violet inside; **spadix** sessile to weakly stipitate, cylindrical to weakly tapered; staminate portion creamy white, protruding forward at anthesis, pointed at apex, 10–17 cm long; pistillate portion whitish, weakly obovoid, 3.5–5.2 cm long (1 cm shorter on back side), 1.1–1.8 mm diam. at apex, 1.5–1.9 mm diam. at middle, (7)17 mm wide at base; staminate portion 6.3–8.1 cm long; fertile staminate portion tapered, 1–1.9 cm diam. at base, 1.2–1.6 cm diam. at middle, 0.9–1.4 cm diam. ca. 1 cm from apex, broadest at the base, slightly constricted above the base; sterile staminate portion as or slightly broader than the pistillate portion, white with tan ring around apex, 0.7–2 cm diam.; pistils (1.6)4–5(8) mm long, (1)2.8–3.2(5.2) mm diam.; ovary (7)8-locular, (1.6)3.3–4(6.7) mm long, 1.5–3(5.2) mm diam., with axile or sub-basal placentation; locules (0.6)1.9–3.4(6.5) mm long, 0.5–0.8(1) mm diam.; ovule sac 1.8(3.5) mm long; ovules 8 per locule, 1–2-seriate, contained within translucent, gelatinous ovule sac, 0.1–0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, style 0.3–0.5 mm long, 1.2–3 mm diam., similar to style type B (rarely C); style apex flat to weakly rounded, sometimes domed; stigma usually hemispheroid, sometimes subdiscoid, pink, 1.2–1.5 mm diam., 0.6–0.7 mm high, covering entire style apex; the androecium truncate, oblong, prismatic, margins irregularly 3–5-sided, sometimes weakly scalloped, 1 mm long, (0.7)2.5–2.7 mm diam. at apex; thecae cylindrical, 0.3 mm wide, ± parallel to one another and contiguous; sterile staminate flowers usually truncate, sometimes clavate or irregularly 5–6-sided, 1.1–2.9 mm long, 0.6–1.8 mm wide. INFRUCTESCENCE 11–17 cm long, 4.5 cm diam.; pistillate spadix 6–8 cm long, 2.5–3.5 cm diam.; berries white, somewhat translucent, 4 per locule, oblong, sticky.

Philodendron radiatum ranges from Mexico (San Luis Potosí to Chiapas and on both Atlantic and Pacific slopes in Chiapas) to Colombia (Antioquia), from sea level to usually no more than 700 m (rare-

ly 1250 to 1860 m; most collections are from below 100 m) elevation. It is perhaps more widespread in South America than collections indicate (only two are known). The plants are very large and difficult to collect and may have been overlooked in other areas.

This species is highly variable morphologically and ecologically versatile as well. In Mexico, it occurs in "Selva Alta Perennifolia," "Selva Mediana," and "Selva Baja Caducifolia" in mesic areas on the Atlantic slope as well as in "Selva Mediana Subperennifolia" and "Selva Baja Subperennifolia" in the drier Yucatán Peninsula. On the Pacific slope it also occurs in areas of "Bosque Pino-Encino." In Central America, this taxon occurs principally in *Tropical moist forest* but also in *Premontane wet forest* and drier parts of *Tropical wet forest.*

Philodendron radiatum is a member of *P.* sect. *Polytomium. Philodendron radiatum* has two varieties, the typical variety having more deeply divided leaf blades with the segments often incised almost to the midrib and variety *pseudoradiatum* with the blades only weakly incised-lobate (less than half the distance to the midrib). While the latter variety is restricted to southwestern Chiapas, even populations of the typical variety on the western slope of Central America have less deeply incised-lobate blades than those on the Atlantic slope. There is also considerable clinal variation in the width of the divisions throughout Central America, with plants in Mexico having, on average, broader pinnae (averaging 4.5 cm wide) than those in Panama, for example, where the pinnae average only about 3 cm wide. Leaves of Mexican populations of *P. radiatum* also consistently lack free basal veins, whereas elsewhere in Central America such veins are present. In western Mexico and Guatemala, plants are also more likely to have longer internodes and to occur more frequently on rocks or creeping over the ground than plants on the more mesic Atlantic slope of Central America.

KEY TO THE VARIETIES OF *P. RADIATUM*

1a. Blades deeply lobed, the divisions near the middle of the blade extending more than ¾ the way to the midrib ..... var. *radiatum*
1b. Blades shallowly lobed, the divisions near the middle of the blade extending less than ½ the way to the midrib ..... var. *pseudoradiatum* (Matuda) Croat

Philodendron radiatum Schott var. **radiatum**

Philodendron augustinum K. Koch, in A. Braun et al., Append. sp. Hort. berol. 1853: 4. 1853–1854. TYPE: Central America. Without exact locality (holotype, B? lost). Schott ic. 2605 (neotype, here designated).

Philodendron polytomum Schott, Bonplandia 7: 164. 1859. TYPE: Mexico. Veracruz: Colipa, Hac. de Sta. Bárbara, *Liebmann s.n.* (holotype, C; isotype, K not seen).

Philodendron impolitum Schott, Prodr. Syst. Aroid. 291. 1860. TYPE: Costa Rica, *Wendland s.n.* (not seen).

Internodes 3–7 cm long, 3–8 cm diam.; cataphylls bluntly to sharply 2-ribbed; **petioles** 33–108 cm long; blades deeply lobed, the divisions near the middle of the blade extending more than ¾ the way to the midrib, 21–101 cm long, 25–90 cm wide; posterior lobes (8)12.5–25 cm long, (9)16–18 cm wide; primary lateral veins 3–8 cm long; basal veins 4(5) per side, (1)2–4 coalesced to 3 cm long, naked 1–6 cm. INFLORESCENCES 1–3(4) per axil; **spathe** 11–25 cm long; **spadix** 10–13 cm long; pistillate portion 3.5–5.2 cm long; pistils (3)4–5(8) mm long; ovaries with axile placentation; style similar to style type B (rarely C).

Flowering in *Philodendron radiatum* var. *radiatum* is documented by few flowering collections made in February, August, and September. Postanthesis collections are common, from every month of the year, and there are no clearly marked differences in the phenology of this species in different parts of Central America. Material was seen at various stages of development from all parts of Central America in about equal numbers. Mature fruits are known only from February and May.

Philodendron radiatum var. *radiatum* is characterized by its moderately thick, mostly short internodes; sharply two-ribbed, deciduous cataphylls; terete petioles; and especially by its deeply incised-lobate leaf blades that mostly linear to linear-lanceolate segments, themselves often lobate toward the base of the blades.

Philodendron radiatum var. *radiatum* might be confused with *P. dressleri* and *P. warszewiczii,* Central American species with incised-lobate leaf blades. *Philodendron dressleri* differs in having thicker leaf blades, more succulent stems with shorter internodes, and especially by having blades that are incised lobate only about midway to the midrib. In addition, *P. dressleri* has one inflorescence per axil and 3–4 locules per ovary, while *P. radiatum* has 1–3(4) inflorescences per axil and 7–8 locules per ovary. *Philodendron warszewiczii* differs by having thinner blades, drying papyraceous with the minor veins distinctly visible. In addition, the lateral leaf blade segments usually have three or more lobes per side. *Philodendron radiatum,* in contrast, has blades drying subcoriaceous with the minor veins rather indistinct and with the

lateral leaf blade segments usually 1–2-lobed per side.

Philodendron radiatum var. *radiatum* has a unique attractant, whose odor profile is made up almost entirely of compounds unique to it, and is pollinated by a new species of *Cyclocephala* (Schatz, 1990).

Additional specimens examined for P. *var.* radiatum. BELIZE. Honey Camp, *Lundell s.n.* (US); Maskall, *Gentle 1141* (MICH, NY); Gracie Rock, 1.5–4 mi. S of Mile 22 on Western Highway, 100 m, *Liesner & Dwyer 1460* (MO); Crooked Tree Village, 60 m, 17°47′N, 88°32′W, *Davidse & Brant 33146* (MO). **Cayo**: Roaring Creek, *Dwyer 12677* (MO); 1.5 mi. W of Augustine, Río Frío, ca. 450 m, *Sutton et al. 211* (BM); Hummingbird Highway, Mile 20, *Dwyer & Liesner 12130* (MO); Chiquibul National Park, Caracol Archaeological Reserve, 550 m, 16°45′N, 89°07′W, *Ingram & Ferrell-Ingram 1935* (MO); Río Ma Cal, San Luis–Cuevas, 1050 ft., *Croat 23534* (MO); Vaca, *Gentle 2552* (MICH). **Corozal**: edge of New River, Pueblo Nuevo, *Gentle 473* (CM, MICH); Cerro Maya Ruins, Lowry's Bright, *Crane 348* (LL); *Gentle 617* (MICH). **Orange Walk**: road to Trinidad, ca. 5 km N of August Pine Ridge, 100 m, 18°N, 88°42′W, 100 m, *Davidse & Brant 32791* (MO); Pulltrouser Swamp, *Lincoln 20* (MO). **Toledo**: Punta Gorda highway, 1 mi. E of junction to San Antonio, ca. 100 ft., *Croat 24512* (MO); Solomon Camp, vic. of Richardson Creek and Bladen Branch junction, Maya Mountains foothills, 80–420 m, 16°32–33′N, 88°45–46′W, *Davidse & Brant 32198* (MO); Columbia Forest Station Area, 1.5 mi. S of Mayan Village of San José, *Croat 24335* (MO); *Holst 4303* (MO). COSTA RICA. **Alajuela**: Cañas–Upala, 10 km N of Bijagua, 200 m, *Croat 36488* (MO). **Heredia**: La Selva Field Station, *Grayum 2534A* (DUKE); 100 m, *3022* (DUKE); *Jacobs 2290* (DUKE); *2707* (MO); 10°26′N, 84°W, *Burger & Stolze 5921* (BM, CR, US); 100 m, 10°26′N, 84°01′W, *Gentry & Ortiz 78615* (MO); Río Sucio, near Puerto Viejo, 20 m, *Croat 35680* (MO); Puerto Viejo–Guápiles, 7 km N of Buenos Aires, 10°23′30″N, 83°48′30″W, *Croat 68386* (MO); Río Sarapiquí, S of La Virgen, 200 m, *Lent 33* (MO); La Tirimbina, 220 m, *Hunter 821* (WIS). **Limón**: Barra del Colorado, N side, 0–2 m, 10°47′N, 83°35′W, *Stevens 24133* (CR, MO); Barra del Colorado–Río San Juan, Laguna de Atrás, 5 m, 10°48-52′N, 83°38′W, *Davidse & Herrera 31512* (CR, MO); Cerro Coronel, E of Laguna Danto, 20–170 m, 10°41′N, 83°38′W, *Stevens 23845* (CR, MO); Parque Nacional Tortuguero, Estación Agua Fría, 2 m, *Robles 1398* (CR, MO); 40 m, 10°26′N, 83°35′W, *1730* (CR, MO); 600 m S, 4 m, 10°32′N, 83°30′W, *1846* (CR, MO); Cahuita, *Poveda 1166* (CR, MO); Cahuita–Limón, 0–10 m, 9°44′N, 83°20′W, *Baker & Burger 157* (CR, NY); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8729* (MO, RSA); *8437* (RSA); Río Colorado, 3.5 airline km S of Islas Buena Vista, 10–120 m, 10°39′N, 83°40′40″W, *Davidse & Herrera 31268* (MO); Barra del Colorado, 1–5 m, 10°47′40″N, 83°25′30″W, *Davidse & Herrera 30882* (MO); Río Pacuare, 50–100 m, 10°15′N, 83°29′W, *Burger & Liesner 6894* (MO); 7 km SE of Bribrí, 100–250 m, *Gomez 20315* (MO); 1 mi. SW of Bribrí, <50 m, *Croat 43228* (CR, MO); vic. of Moin, 0 m, 10°N, 83°04′W, *Croat 61207* (MO); Bahía de Portete Parque Nacional, 0–10 m, 10°N, 83°05′W, *Thompson & Rawlins 1175* (CM); Río Reventazón, Finca Montecristo, below Cairo, 25 m, *Standley & Valerio 48969* (US). EL SALVADOR. La Cebadilla, *Calderón 1245* (US). **San Salvador**: Tonacatepeque vicinity, *Standley 19538* (GH, NY, US); *Calderón 201* (GH, NY, US). GUATEMALA. **Alta Verapaz**: *Tuerckheim 8330* (US); eastern portions of Verapaz and Chiquimula, *Watson 194* (GH); near Finca Sepacuite, *Cook & Griggs 724* (US); Cubilquitz, 350 m, *Tuerckheim 8330* (US); Guatemala–El Estor, 5 mi. W of Tucurú, 600 m, *Croat 41509* (MO); Tucurú–El Estor, Finca Argentina, above Papalha, 15 mi. W of Telemán, 550–650 m, *Croat 41550* (MO); ca. 6 km NE of Panzós, 500 m, *Croat 41616* (MO). **Izabal**: Quiriguá vicinity, 75–225 m, *Standley 23939* (US); ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41803* (MO); Río Frío, Cerro San Gil, 75–150 m, *Steyermark 41534* (MO, NY); W of El Estor and abandoned nickel mine, 1–10 m, *Stevens & Martínez 25283* (MO). **Petén**: La Libertad, *Lundell 2645* (MICH, NY); El Paso, *Lundell 1571* (MICH); Uaxactun, *Bartlett 12702* (MICH); Tikal National Park, *Contreras 105* (LL). **Quezaltenango**: along CA-2, 4 mi. NW of turnoff to Coloba, *Croat 32767* (MO); Coatepeque–Retalhuleu, Hwy. CA-2, 3 mi. S of turnoff to Colomba, 600 m, *Croat & Hannon 63414* (MO, US). **Sacatepéquez**: Volcán Santa Clara, 1250–2650 m, *Steyermark 46621* (MO). HONDURAS. Puerte Sierra, *Wilson 321* (NY). **Atlántida**: Lancetilla Valley, near Tela, *Standley 52945* (US); *53668* (US); *53985* (US); ca. 10 mi. SE of Tela, Río Lancetilla, 10–150 m, *Croat 42631* (MO); Río Cangrejal, 5 km inland from La Ceiba, *Blackmore & Chorley 4155* (BM, MO, UNAH); Río Sambo, Tocoa–La Cieba, 11.3 mi. from Río Cangreja Bridge at La Ceiba, 30 m, 15°47′N, 86°30′W, *Croat & Hannon 64581* (BM, MO); Parque Nacional Pico Bonito, ca. 10 km SW of La Ceiba, 160 m, 15°42′N, 86°51′W, *Evans 1675* (MO). **Colón**: Río Negro, Trujillo, *Clewell et al. 4345* (MO). **Copán**: ca. 4 mi. E of Copán, 800 m, *Croat 42502* (MO); 10 mi. W of Copán, road to La Entrada, 700 m, *Croat 42516* (MO). **Cortés**: Lago Yojoa, Punta del Cacao, 650 m, 14°05′30″N, 87°58′W, *MacDougal et al. 3079* (MO); Ocote Arrancado, 50 km N Lago de Yojoa, *Nelson et al. 5868* (MO, VBD); Puerto Cortes–Guatemalan border, 2–3 mi. SW of Omoa, *Croat 42558* (MO); N of Lago de Yojoa, along old Highway 1, ca. 2–6 mi. from junction with new Highway 1, SW of Santa Cruz de Yojoa, 600 m, *Croat 42745* (MO). **Gracias a Díos**: Río Plátano Biosphere Reserve, Las Marías (Batil Tuk), 30 m, *Knees et al. 2825* (BM). **Morazán**: El Zamorano, 800 m, *Molina 34353* (MO). **Olancho**: El Jocomido–Cerro El Mulato, *Blackmore & Heath 1686* (BM, MO); Gualaco–San Esteban, Río Olancho, 7.4 mi. NE of San Esteban, 540 m, 15°20′N, 85°42′W, *Croat 64365* (K, MO, NY). **Santa Bárbara**: Lago Yojoa, Punta Gorda, 650 m, 14°52′N, 88°W, *MacDougal et al. 3126* (MEXU, MO, NY); 630 m, 14°53′N, 88°W, *Liesner 26769* (MO); 700 m, *Croat 42752* (MO); El Novillo, 640 m, 14°53′N, 88°00′30″W, *Evans 1044* (MO). **Yoro**: Aguán River Valley, Coyoles, *Yuncker et al. 8624* (GH, MO, NY, UC, US). MEXICO. Location unspecified, Reko 3690 (US); *Sandoval 14* (US). **Campeche**: Mpio. Hopechén, Rancho El Carmen, 33–35 km S of Xmaben on road from Hopelchén to Xpujil, near Xpanzil, 200 m, 18°58′N, 89°20′W, *Sanders et al. 9735* (MO); Huatusco, *Sandaval 14* (US); Patria, *Engler 197* (BM, GH); Santa Leonor, E of Río San Pedro, *Barlow 16/8* (BH). **Chiapas**: San Manuel, ca. 15 km above Palenque, on road to Ocosingo, ca. 500 m, *Madison 7312* (SEL); Escuintla–El Triunfo, 1 mi. N of Escuintla, 100 m, *Croat 43811* (MEXU, MO); Esperanza–Escuintla, *Matuda 16662* (F, MEXU); *17788* (NY); 150 m, *18045* (MEXU);

Tapachula–Nueva Alemán, 4 mi. N of Tapachula, 250 m, *Croat 43794* (MO); Escuintla–El Triunfo, ca. 8.5 mi. NE of Escuintla, 250 m, *Croat 43820* (MO); Escuintla–Monte Ovando, 2.8 km NW of Turquiz, ca. 100 m, *Croat 47511* (MO); Acacoyagua, Cerro Ovando, 800–900 m, *Croat 78548* (CHIP, MO); Huixtla–Motozintla de Mendoza, 4.8 km N of Huixtla, ca. 200 m, *Croat 47523* (MO); 2 mi. S of Chiapas border, along Hwy. 195, 8 mi. N of Pichucalco, 80 m, *Croat 40088* (MO); 5 mi. SE of Palenque, on road to Ocosingo, 200 m, *Croat 40135* (MO); Palenque–Bonampak, 89–90 mi. SW of Palenque, 350–370 m, *Croat 40217* (MO); 73 mi. SE of Palenque, 460 m, *Croat 40267* (MO); Ocozocoautla–Apitpac, 20 mi. N of Ocozocoautla, 700 m, *Croat 40650* (MO); 5 mi. N of Ocozocoautla, 1000 m, *Croat 40543* (MO); Motozintla de Mendoza–Huixtla, 15 mi. S of Motozintla de Mendoza, 900 m, *Croat 40765* (MO); Mpio. Ixtacomitan, 7 km SW of Ixtacomitan, 250 m, *Breedlove 45915* (MO); Mpio. Mapastepec, Sierra de Soconusco, new unfinished road to Tuxtla Gutiérrez, 200 m, 15°31′N, 92°50′W, *Croat 63382* (B, K, MO, NY, US); Mpio. Ocosingo, Lacanja–Chanzayab, Palenque–Boca Lacantum, 340 m, *Martínez 15071* (MO); Laguna Ocotalito, 12 km N of Monte Líbano, trail to Chancala, 980 m, *Martínez 17029* (MO); Bonampak, 520 m, *Breedlove & Almeda 58051* (MO); Mpio. Palenque, 8–9 km S of Palenque, 300 m, *Breedlove & Strother 46895* (CAS); 25 km S of Palenque, 300 m, *Breedlove & Almeda 57318* (CAS); Mpio. Tzimol, 15 km S of Comitán, 1200 m, *Breedlove 53732* (CAS). **Oaxaca**: *Williams 9173* (US); 14 mi. S of Tuxtepec, *Moore & Bunting 8904* (BH, MO); *8910* (BH); Tuxtepec–Oaxaca, 0.5 mi. S of Valle Nacional, Highway 175, 120 m, *Croat 39700* (MO); 3 km S of Hidroeléctrica Temascal, 50 m, *Cortés et al. 875* (MO); Uxpanapa region, Esmeralda–Río Verde, 1.1 mi. S of Esmeralda, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63234* (MO); Jalpan, 2–3 km E of La Baquilla, Río Santa María, 270–320 m, *Carranza & Zamudio 4548* (MO); ca. 1.5 km E of La Boquilla, 270–320 m, *Carranza & Díaz 4721* (MO). **San Luis Potosí**: Highway 85, 6 mi. NW of Tamazunchale, 250 m, *Croat 39262* (MO); Tamazunchale, *Edwards 626* (DS, MO). **Tabasco**: 30 mi. E of Minatitlán, *Barkley & Carr 36221* (GH); Alemán, 10 mi. NW of Cardenas, *Barlow 26/25* (BH); Mpio. Cárdenas, vic. Cárdenas, *Cowan 2021* (MO); Mpio. Huimanguillo, km 12.6 de la desviación de Huimanguillo, *Cowan & Magaña 3255* (CAS, NY). **Veracruz**: Huatusco–Puente Nacional, El Mirador, 21 km E of Huatusco, ca. 1200 m, *Croat 43974* (MO); *Moore & Bunting 8855* (BH); Playa Escondida, N of Sontecomapan, along Caribbean cliffs, 10–60 m, *Gentry et al. 32610* (MO); Córdoba–Veracruz, San José de Gracia, ca. 750 m, *Croat 39612* (MO); Highway 180, 6 mi. E of Coatzacoalcos, *Croat 40064* (MO); NW of Misantla, 2.4 mi. on road to Martínez de la Torre, ca. 320 m, *Moore & Bunting 8946* (BH); Dtto. Papantla, *Kelly 126* (BH); Mpio. Coatepec, 5 km by air SE of Tuzamapan, 680 m, 19°21′N, 96°50′W, *Nee & Taylor 26026* (NY); Mpio. Cosamaloapan, 10 km by air NW of Tres Valles, 25 m, 18°17′N, 96°13′W, *Nee & Taylor 29306* (NY); Mpio. Hidalgotitlán, 1 km SE of Agustín Melgar, 100 m, 17°15′N, 94°33′W, *Nee 29765* (NY); Mpio. Naolinco, 2 km from Concha al Espinal, 900 m, *Ortega 630* (MO). **Yucatán**: Izamal, 20°56′N, 89°01′W, *Gaumer 23200* (GH, NY, US); *1413* (GH, MO); Uayma, *Schott 766* (BM). NICARAGUA. **Boaco**: Boaco–Camoapa, N slope of Cerro Mombachito, 500–900 m, ca. 12°24–25′N, 85°32–33′W, *Stevens & Grijalva 14699* (MO); Hwy. 33, vic. Río Quilan bridge, ca. 300–310 m, 12°35′N, 85°32′W, *Stevens 9330* (BM, MO). **Chontales**: Juigalpa–La Libertad, ca. 17.4 km NE of Río Mayales, at ford of Río El Bizcocho, 350–400 m, ca. 12°12′N, 85°17′W, *Stevens 4093* (BM, MO); *4095* (BM, MO); ca. 2.8 km above Cuapa, 400–500 m, ca. 12°17′N, 85°23′W, *Stevens 3671* (MO, PMA). **Estelí**: km 167 on Hwy. 1, ca. 15.8 km N of entrance to Estelí, 825–850 m, ca. 13°15′N, 86°22′W, *Stevens 5788* (MO). **Jinotega**: Río Bocay, Salto Acatulu, ca. 130 m, 14°13′N, 85°10′W, *Stevens et al. 16749* (MO). **Madriz**: Cerro Quisuca, 1100–1250 m, ca. 13°30′N, 86°31′W, *Stevens & Grijalva 16063* (MBM, MO). **Managua**: Ciudad Managua, Reparto Bolonia, *Guzmán et al. 1071* (MO). **Nueva Segovia**: Río San Fernando Valley, ca. 5.2 km N of San Fernando, 13°2–3′N, 86°19–20′W, *Stevens 3245* (BM, MO). **Río San Juan**: Río Santa Cruz–Caño Santa Crucita, La Palma, 40–60 m, 11°2–4′N, 84°24–26′W, *Stevens 23427* (MO); Caño Chontaleño, 20 km NE of El Castillo, 200 m, *Neill & Vincelli 3620* (MO). **Zelaya**: La Barra de Punta Gorda, 0–2 m, 11°30′N, 83°46′W, *Moreno 13225* (MO); Caño Montecristo, mouth of Caño El Consuelo, ca. 10 m, 11°35′N, 83°51′W, *Moreno 15027* (MO); 6.5 km al SE de Waslala, 520–560 m, 13°16′N, 85°24′W, *Moreno 17288* (MO); Puerto Cabezas–Rosita, ca. km 47, ca. 5.3 km W of Río Wawa Ferry, <10 m, 14°06′N, 83°35′W, *Stevens 8568* (MO); along road to Panua, 2.3–3.1 km NW of Panua, 4.2–5 km from main road, 30–40 m, 14°18–19′N, 83°41–42′W, *Stevens 7796* (MO); Puerto Cabezas–Río Wawa, Ibo Tingni, drainage of Caño Sung Sung, <10 m, 14°9–11′N, 83°29–31′W, *Stevens 10658-a* (MO); Auastara vicinity, <10 m, ca. 14°19′N, 83°12–13′W, *Stevens 10441* (MO); SW of Bluefields, 10–40 m, 12°N, 83°46′W, *Stevens 19781* (MO); 6.3 km S of bridge at Colonia Yolania, on road to Colonia Manantiales of Nueva Guinea, 200–300 m, *Vincelli 249* (MO); 40–45 km SW of Waspam, 10–100 m, *Atwood 3717* (MO); Cerro Livico, 7 km NE of Siuna, 500 m, *Neill 3634* (BM, MO); Cerro Waylawás, ca. 80 m, 13°39′N, 84°49′W, *Pipoly 4370* (MO); ca. 100–200 m, 13°38–39′N, 84°48–49′W, *4239* (MO); *4162* (MO); ca. 100–268 m, ca. 13°39′N, 84°48–49′W, *Stevens 7378* (MO); Caño Costa Riquita, ca. 1.8 km SW of Colonia Naciones Unidas, 150–180 m, ca. 11°43′N, 84°18′W, *Stevens 5081* (MO); Cerro Saslaya–San José del Hormiguero, between Caño Sucio and Loma Mollejones, ca. 300–450 m, 13°45′N, 84°58–59′W, *Stevens 7011* (MO); Cayo Palmeta, 0–10 m, 11°34′N, 83°39′W, *Stevens 20765* (MO); San Juan del Norte, *Smith 22* (MO); *Seymour 5906* (MO); Cerro Baká, ca. 6.5 km E of Río Coperna, 200–320 m, 13°40′N, 84°30′W, *Pipoly 4846* (MO); Estación Experimental El Recreo, W de Cerro La Ceiba, 12°10′N, 84°18′W, *Sandino 1656* (MO); Monkey Point, Caño El Pato, ca. 10 m, 11°35′N, 83°42″W, *Moreno 12399* (MEXU, MO); 1–5 m, 11°36′N, 83°40′W, *12318* (MO); 1–5 m, 11°36′N, 83°38′W, *Moreno & Sandino 12007* (MO); 0–20 m, 11°35′N, 83°39′W, *Stevens 20031* (MO); 1 km S of Monkey Point, ca. 5 m, 83°39′W, 11°35′N, *Moreno & Sandino 12541* (MO); Río Likas, near Silima Lila, 50 m, ca. 14°30′N, 83°50′W, *Pipoly 4097* (MO); Río Prinzapolka, 0.3–1.9 km N of Limbaika, 8–10 m, ca. 13°29′N, 84°13′W, *Stevens 8264* (MO); ca. 2 km S of Waní, ca. 0–100 m, ca. 13°42′N, 84°50′W, *Pipoly 4729* (MO); Río Punta Gorda, Atlanta, 10 m, 11°33′N, 84°02′W, *Moreno & Sandino 12808* (MO); Atlanta, 2 km S of Carolina del Sur, ca. 60 m, 11°32′N, 84°01′W, *Moreno & Sandino 12890A* (MO); Río Rama, Caño Zamora, ca. 10 m, 11°57′N, 84°16′W, *Stevens 8849* (MO); Río Sucio, E of Bonanza, ca. 140 m, 14°01′N, 84°34′W, *Stevens 12345* (MO); Río Waspuk, 75–100 m, 14°15′N, 84°36′W, *Stevens*

13091 (MO). PANAMA. Ahorca Lagarto, *Cowell 262* (NY). **Bocas del Toro**: Gualaca–Chiriquí Grande, 4.2 mi. S of Chiriquí Grande, 8°55′N, 82°09′W, *Croat 66816* (AAU, CM, F, MO); Changuinola–Almirante Railroad, Milla 7.5, 100 m, *Croat & Porter 16433* (MO); *Croat 38122* (MO); Chiriquí Lagoon, Water Valley, *von Wedel 989* (GH, MO); Isla Colón, Swan Key, 2 km N, *Tyson & Loftin 6307* (FSU, MO); Río Cricamola, Finca St. Louis–Konkintoë, *Woodson et al. 1901* (GH, MO, NY); Río Changuinola, ca. 1 km above mouth of Río Teribe, <100 m, 9°21′40″N, 82°31′40″W, *Croat & Zhu 76446* (CM, MO). **Canal Area**: *Hayes 805* (NY); Gorgona–Gatún, 10–15 m, *Pittier 2300* (US); Gatún, *Standley 27023* (US); Ft. Sherman, *Standley 30992* (US); Frijoles, *Standley 27467* (US); Ft. Randolph, *Standley 28626* (US); 66–70 m, *Dodge et al. 16870* (MO, U, UC); near Gatún, *Standley 27203* (US); vic. Summit Garden, *Tyson & Lazor 6121* (FSU, RSA); Barro Colorado Island, Gatún Lake, *Standley 31328* (US); *40818* (US); *Kenoyer 178a* (US); *Elmore X14* (MICH, RSA, US); *Croat 7178* (MO); 79°49′46″W, 9°09′56″N, *6124* (MO, NY, SCZ); *6060* (MO); *4655* (MO, SCZ); *Aviles 44* (MO); *Shattuck 266* (GH, MO); Navy Pipeline Road, *Smith & Smith 3313* (US); 0.25 km NW of Río Macho bridge, 10 km NW of Gamboa, 125 m, *Nee 7863* (MO, RSA, TEX). **Chiriquí**: Gualaca–Chiriquí Grande, 13.6 mi. N of Continental Divide, 120 m, 8°57′N, 80°56′W, *Croat 74934* (MO). **Coclé**: 27 km N of Penonomé, on road to Coclesito, at Continental Divide, 1500 ft., *Hammel 1648* (SEL, MO); Llano Grande–Coclesito, 12 mi. from Llano Grande, 200 m, 8°47′N, 80°28′W, *Churchill et al. 3987* (RSA). **Colón**: ca. 8 km E of Piña, 50–100 m, 9°17′N, 80°W, *Thompson 4815* (CM, MO); Río Indio–Miguel de la Borda, 0 m, *Croat 36927* (MO); near Nuevo Tonosí, 2 mi. from Portobelo, on road to Nombre de Dios, <100 m, *Croat 33527* (MO); Santa Rita Ridge, Transisthmian Highway, ca. 10 mi. from hwy., *Porter et al. 4738* (MO); ca. 7 mi. from Transisthmian Highway, ca. 650 ft., *Wilbur et al. 15083* (MO); Santa Rita Trail, *Cowell 106* (NY). **Panamá**: ca. 20 km from Inter-American Highway, N of Cerro Azul, *Mori et al. 3786* (MO); Río Terabe Valley, El Llano–Cartí, 8 km from Pan-American Highway, 300–400 m, 9°16′N, 79°W, *Knapp & Schmalzel 5476* (MO). **San Blas**: Isla Playón Chico, 0–50 m, 9°20′N, 78°13′W, *Herrera 369* (MO); Nusagandi, El Llano–Cartí Road, 9 mi. N of main highway, 350 m, 9°20′N, 79°W, *Croat & Zhu 76566* (MO, SEL). **Veraguas**: Santa Fe–Río Calovébora, 0.6 mi. beyond agricultural school near Santa Fe, 735 m, *Croat 32982* (MO).

Philodendron radiatum var. **pseudoradiatum** (Matuda) Croat, stat. et comb. nov. Basionym: *Philodendron pseudoradiatum* Matuda, Revista Soc. Mex. Hist. Nat. 1: 96, fig. 8. 1950. TYPE: Mexico. Chiapas: Mun. Escuintla: Turquía, Salto de Agua, 8 Sep. 1947, *Matuda 17787* (holotype, MEXU; isotypes, DS, NY, UC). Figures 8, 327–330.

Internodes 2–12 cm long, 1–2.5 cm diam.; cataphylls unribbed; **petioles** 28–78 cm long; **blades** shallowly lobed, the divisions near the middle of the blade extending less than ½ the way to midrib, 11–60 cm long, 11–42 cm wide; posterior lobes (8)12.5–25 cm long, (9)16.2–18 cm wide; basal veins 5(7–8) per side, with 0–1 free to base, posterior rib absent; primary lateral veins 3–5 per side. INFLORESCENCES 1 per axil; **spathe** 12–18 cm long; **spadix** 12.8–17 cm long; pistillate portion 4–4.5 cm long; pistils 1.6–2.2 mm long; ovary with sub-basal placentation; style similar to style type B.

The flowering phenology of *Philodendron radiatum* var. *pseudoradiatum* is still poorly known. Flowering collections are known only from January and September, but the flowering pattern is probably just poorly documented rather than bimodal.

Philodendron radiatum var. *pseudoradiatum* is endemic to Mexico, where it is known only from southwestern Chiapas, at 200 to 350 m elevation in "Selva Alta Perennifolia."

Philodendron radiatum var. *pseudoradiatum* is distinguished by its incised-lobate blades with the lobes divided less than halfway to the midrib. The typical variety generally has the blades incised more than three-fourths of the way to the midrib.

This taxon might be confused with *P. dressleri*, which also has leaf blades divided only about halfway to the midrib. That species differs in having much thicker stems (typically to 6 cm diam.), sharply 2-ribbed cataphylls, and by occurring in much drier areas where it loses its leaves during the dry periods. In contrast, *P. radiatum* var. *pseudoradiatum* has rather slender stems, unribbed cataphylls and occurs in mesic areas.

Until recently, *Philodendron radiatum* var. *pseudoradiatum* was represented by only two collections, *Matuda 17787* and *18718*, from the same locality. Several collections are noteworthy. *Matuda 18045* consists of two sheets, one of which has a leaf lobed in much the same manner as the type, while the other has a leaf lobed to more than two-thirds of the way to the midrib. This may be an indication that the type of *P. radiatum* var. *pseudoradiatum* is merely an aberration in the degree of lobing for *P. radiatum*.

Another noteworthy collection is *Croat & Hannon 63381* from Sierra de Soconusco, northwest of Mapastepec. It is perhaps also *P. pseudoradiatum* but has smaller and narrower leaves. It looks much like a hybrid between *P. radiatum* var. *pseudoradiatum* and some other species, but if so, it is not clear which other species might be involved in the putative hybrid plant.

Additional specimens examined. MEXICO. **Chiapas**: Escuintla, Salto de Agua, 350 m, *Matuda 18718* (MEXU, UC); Mpio. Mapastepec, Sierra de Soconusco, new unfinished road to Tuxtla Gutiérrez, 200 m, 15°31′N, 92°50′W, *Croat & Hannon 63381* (CAS, CM, F, MEXU, MO, TEX).

Philodendron roseospathum Croat, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, along road just below the summit, 9°15′N, 79°30′W, 17 June 1976, *Croat & Zhu 76211* (holotype, MO–4619415; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, GH, HUA, K, M, MEXU, NY, P, PMA, RSA, S, SEL, TEX, US, VEN). Figures 341–345.

Planta terrestris, raro hemiepiphytica; internodia 1–4 cm longa, 1.5–2.7 cm diam.; cataphylla 12–27 cm longa, acute 2-costata, persistentia semi-intacta nodis superioribus; petiolus U-formatus, obtuse sulcatus, 10–23 cm longus, 3–6 mm diam., crassior quam latus; lamina (22)30–49 cm longa, 9.8–21 cm lata, elliptica vel oblongo-elliptica, interdum oblanceolata, interdum attenuata apice, acute vel anguste rotundata, interdum attenuata basi; inflorescentia 1–2; pedunculus 2.5–6 cm longus; spatha 6.5–10 cm longa; lamina spathae extus saepe rubella plerumque atriviridi, intus pallide viridi vel marronina; tubo spathae extus pallido-lineato, intus pallide viridi vel marronino; pistilla (4)5–7(8)-locularia; loculi 14–18-ovulati; baccae albae.

Terrestrial or rarely hemiepiphytic; stem appressed-climbing or creeping, leaf scars inconspicuous, obscured by cataphyll fibers; internodes short, semiglossy, 1–4 cm long, 1.5–2.7 cm diam., longer than broad, dark green to gray-green to reddish, obscured by cataphyll fibers; roots many, thin, wiry, descending, greenish brown; cataphylls 12–27 cm long, sharply 2-ribbed (unribbed to weakly to sharply 2-ribbed in Colombia), pale red to purple-violet, drying dark brown, sharply D-shaped, persisting semi-intact at upper nodes, as fibers below; **petioles** 10–27 cm long, 3–6 mm diam., U-shaped, thicker than broad, firm, dark green to reddish, tinged purple, somewhat flattened to obtusely or narrowly sulcate adaxially; geniculum pale green to reddish violet, 1 cm long, 1.5 cm diam.; **blades** elliptic to oblong-elliptic, sometimes oblanceolate, rarely elliptic, coriaceous to subcoriaceous, conspicuously bicolorous, sometimes acuminate at apex (the acumen inrolled, 1–3 mm long), acute to narrowly rounded, sometimes attenuate at base, (22)30–49 cm long, 9.5–21 cm wide (1.8–3.5(4.5) times longer than broad), (1.6–3.2 times longer than petiole), about twice as long as wide, upper surface dark green, matte to semiglossy, lower surface moderately paler, semiglossy to glossy; midrib narrowly sunken, paler than surface above, narrowly convex, thicker than broad, matte, paler than surface and sometimes reddish green below; basal veins lacking or sometimes 1–2 per side, free to base; primary lateral veins 8–14(16) per side, departing midrib at a 40–55° angle, sunken to narrowly sunken, concolorous to paler than surface above, convex and darker than surface below; interprimary veins few, sunken to narrowly sunken, concolorous to paler than surface above, raised and darker than surface below; minor veins few, moderately obscure above, darker than surface below, arising from midrib only, sometimes prominulous and weakly undulate on drying. INFLORESCENCES 1–2 per axil; peduncle 2.5–6 cm long, 2.5–5 mm diam., reddish, prominently green streaked; **spathe** 6.5–10 cm long (1.3–3.3(4.6) times longer than peduncle), red to maroon or violet-purple or sometimes green heavily tinged red, sometimes greenish white throughout; spathe blade frequently dark green (red in Colombia) outside, pale green to maroon inside; spathe tube short pale-lineate outside, 3–4 cm long, 2 cm diam., pale green to maroon inside; **spadix** ± tapered, 6.8–8 cm long, broadest at the base; pistillate portion white to pale green, cylindrical, 2–3.7 mm long, 1–1.5 mm diam. at apex, 11–7.2 mm diam. at middle, 9–11(17) mm wide at base; staminate portion 3.9–4.9(6) cm long; fertile staminate portion cream, cylindrical to somewhat tapered, 10 mm diam. at base, 8 mm diam. at middle, 8 mm diam. ca. 1 cm from apex, broadest usually at base, narrower than the pistillate or sterile portion; sterile staminate portion as broad as the pistillate portion, 10 mm diam.; pistils 2.5 mm long, 1.6–1.9 mm diam., tinged reddish; ovary (4)5–7(8)-locular, 1.4 mm long, 1.6 mm diam., with axile placentation; locules 1.4 mm long, 0.5 mm diam.; ovules 14–18 per locule, contained within a gelatinous matrix, 2-seriate, 0.3–0.5 mm long, longer than funicle; funicle 0.2–0.4 mm long, adnate to lower part of partition, style 0.4–0.6 mm long, 1.6–1.8 mm diam., similar to style type B; style apex flat to weakly rounded; stigma usually subdiscoid, 1.1–1.3 mm diam., 0.2–0.5 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 0.7 mm long, 1.2–1.5 mm diam. at apex; thecae oblong to cylindrical, 0.5 mm wide, ± parallel to one another and contiguous; sterile staminate flowers clavate, blunt, irregularly 4–6-sided, 2.3 mm long, 2 mm wide. INFRUCTESCENCE with pistillate spadix 4–4.5 cm long, 1.5–2.5 cm diam.; berries white (immature), 3.5 mm long, 2.6 mm diam., 12–14 per locule; seeds 7–9 per locule, whitish, oblong, 1.8 mm long, sharply tapered on one end.

Philodendron roseospathum ranges from Panama to Colombia. In Panama, this taxon is restricted to both sides of the Panama Canal, ranging from Ver-

aguas to San Blas, mostly in *Premontane rain forest* or less frequently in *Tropical wet forest* life zones, at 350 to 1000 m elevation. In Colombia, it has been collected only in tropical pluvial forest at 100 to 900 m.

Philodendron roseospathum is a member of *P.* sect. *Philodendron* subsect. *Canniphyllum*. The typical variety is recognized by its generally erect, frequently terrestrial habit, short internodes, and rosulate cluster of leaves with moderately short, bluntly sulcate, thicker-than-broad petioles. The dark green, elliptic-oblanceolate leaf blades are narrowly rounded to acute at the base. It is especially recognizable by its masses of weathered persistent cataphylls and clusters of inflorescences with reddish spathes (hence the name "roseospathum"). This species is unusual for the genus in that it is generally terrestrial. It has prospered in cultivation and is deemed an important horticultural introduction.

Philodendron roseospathum appears to be most closely related to *P. cuneatum* Engl. from the Pacific slope of Colombia, but the latter species differs in having acutely sulcate, C-shaped petioles and smaller, more narrowly pedunculate inflorescences with white spathe blades. It is also related to several other undescribed species from the Amazon basin.

Philodendron roseospathum is here divided into two varieties, with variety *angustilaminatum* Croat differing from the typical variety in having somewhat longer petioles and proportionately much narrower blades (4.5 times longer than broad vs. an average of 2.5 times longer than broad for the typical variety). See *P. roseospathum* var. *angustilaminatum* for additional differences.

KEY TO THE VARIETIES OF *P. ROSEOSPATHUM*

1a. Blades oblong, ca. 4.5 times longer than wide; Panama (Colón), 915 m elevation ..... var. *angustilaminatum*

1b. Blades ± elliptic, ca. 2.5 times longer than wide; Panama to Colombia, 400–900 m elevation ..... var. *roseospathum*

Philodendron roseospathum Croat var. **roseospathum**

Flowering in *Philodendron roseospathum* var. *roseospathum* occurs in the late dry season and early rainy season (March through July) with post-anthesis collections known from March through September and immature fruits from July to December. The few South American collections concur with this pattern. Flowering collections are known from Colombia in July.

In Central America, *P. roseospathum* var. *roseospathum* is common locally in cloud forests along the Continental Divide as far west as Veraguas and as far east as the El Llano-Cartí Road. It is certainly to be expected in Darién Province.

For differences with *P.* var. *angustilaminatum*, see the preceeding key.

Additional specimens examined for P. roseospathum *var.* roseospathum. PANAMA. **Coclé**: Continental Divide ridge, Coclesito Road, *Hammel 2540* (CR, MO); El Copé region, 7 km N of Copé, Alto Calvario, 800 m, *Folsom & Mauseth 7948* (MO); 750–900 m, *Croat 44738* (F, MO); 710–800 m, 8°39′N, 80°36′W, *68763* (MO); 900–1000 m, 8°39′N, 80°36′W, *Croat 75057* (MO); El Valle region, La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, *Croat 67130* (CAS, CM, K, MEXU, MO, NY, PMA, TEX); 860–900 m, *37346* (F, MO); 830–900 m, 8°36′N, 80°07′W, *74810* (CM, LE, MO, WIS); ca. 800 m, *25435* (F, MO); *Luteyn & Kennedy 1652* (MO); 850 m, 8°37′N, 80°06′W, *de Nevers et al. 3513* (MO); 2700 ft., *Sytsma et al. 4350* (CM, MO); 840–880 m, 8°38′N, 80°7.5′W, *Grayum & Evans 9908* (MO); Cerro Gaital, 900–1000 m, 8°40′N, 80°07′W, *Knapp 5311* (MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76734* (AAU, CAS, CM, MEXU, MO); N slope and summit of Cerro Pilón, 900–1173 m, *Croat 22951* (MO). **Panamá**: El Llano–Cartí Road, 4 mi. beyond the highway, 500 m, *Croat 49135* (MO); Cerro Jefe region, 750–850 m, 9°15′N, 79°30′W, *McPherson 11166* (MO), *11197* (CM, MO); 1000 m, *Croat 49088* (MO); ca. 1000 m, *Mori et al. 3795* (MO); ca. 950 m, ca. 9°15′N, 79°30′W, *McPherson 7107* (B, K, MO, US); 2500–3000 ft., *Hammel 3704* (MO); 750–800 m, 9°14′N, 79°22′W, *Croat 67089* (MO); vic. Altos de Pacora, 800–1000 m, *Croat 22672* (CM, L, MO, WIS); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68635* (MO); La Eneida, ca. 800 m, *Kennedy et al. 3374* (US); *Plowman & Weil 3158* (ECON); 1000 m, *Folsom & Page 5938* (MO); 6 mi. above Lago Cerro Azul, *Croat 15225* (MO); Campo Tres, ca. 700 m, *Croat 27069* (F, MO); 4.6 km beyond peak, on road to Altos de Pacora, 26.3 km from the Inter-American Highway, ca. 600 m, *Croat 35931* (CAS, CM, F, GH, M, MEXU, MO, P). **San Blas**: El Llano–Cartí Road, Nusagandi, 300–350 m, 9°15′N, 79°W, *Croat 69282* (MO); Mile 10.9, 450 m, 9°18′N, 79°59′W, *Croat 75123A* (MO); Cerro Obu, 400–500 m, 400–500 m, *de Nevers et al. 8054* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río San Luis, past Escuela Agrícola Alto de Piedra, ca. 5 mi. N of school, 670 m, 8°33′N, 81°08′W, *Croat 66972* (GB, MO, RSA); Santa Fe–Calovébora, 1.7 mi. past Alto Piedra School, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76857B* (MO).

COLOMBIA. **Antioquia**: Parque Nacional Natural "Las Orquídeas," Sector Venados, 900 m, 6°33′N, 76°19′W, *Cogollo et al. 3344* (MO). **Chocó**: Quibdó–Istmina, vicinity of Quibdó, <100 m, 6°28′N, 76°36′W, *Croat & Cogollo 52233* (MO); Quibdó–Bolívar, 117–118 km E of Quibdó, 465 m, 5°44′N, 76°28′W, *Croat 57515* (CHOCO, CM, COL, JAUM, MO, NY, PMA); Río Baudó, *Fuchs et al. 22048* (COL); Medellín–Quibdó at Km 208.5, 9 km W of Tutunendo, ca. 9 km E of Quibdó, <100 m, 5°39′N, 76°40′W, *Croat 56202*.

Philodendron roseospathum Croat var. **angustilaminatum** Croat, var. nov. TYPE: Panama. Colón: Cerro Bruja as approached from Río Escandaloso, 915 m, 18 May 1978, *Hammel 3133* (holotype, MO–2639732). Figure 349.

Internodia brevia; cataphylla ignota; petiolus 24–27 cm longus; lamina oblonga, 42–46 cm longa, 9.5–10 cm lata, circa duplo longior quam petiolus; pedunculus 3.8 cm longus; spatha 7 cm longa, omnino viridalba; pistilla (4)5-locularia; loculi 6–8-ovulati.

Internodes short; cataphylls not seen; **petioles** 24–27 cm long; **blades** oblong, acuminate at apex, rounded at base, 42–46 cm long, 9.5–10 cm wide (4.2–4.8 times longer than wide), (1.75 times longer than petiole); basal veins 2 per side, free to base; primary lateral veins 10 per side. INFLORESCENCES with peduncle 3.8 cm long; **spathe** 7 cm long greenish white throughout; spathe tube 3 cm long; **spadix** 6.3 cm long; pistillate portion 2 cm long in front; staminate portion 4.3 cm long; pistils 1.7 mm long; ovary 4(5)-locular; ovules 6–8 per locule, 1-seriate, ca. 0.3 mm long; style similar to style type D. Berries unknown.

Flowering in *Philodendron roseospathum* var. *angustilaminatum* probably occurs in the wet season, with the only flowering collection from May.

Philodendron roseospathum var. *angustilaminatum* is known only from the type locality near the Canal Area in Colón Province, at 915 m elevation in *Premontane rain forest.*

This variety is distinguished by its long-petiolate, oblong leaf blades with rounded bases and greenish white spathes. It is distinguished from the typical variety by its proportionately much narrower blades (4.5 times longer than wide in *P. roseospathum* var. *angustilaminatum* vs. about 2.5 times longer than wide in var. *roseospathum*) and proportionately longer petioles (only 1.7 times longer than petiole vs. 1.6–3.2 times longer in var. *roseospathum*). In addition, *P. roseospathum* var. *angustilaminatum* has only 6–8 ovules per locule (vs. 16–18 for *P. roseospathum* var. *roseospathum*).

It is unusual that *P. roseospathum* var. *angustilaminatum* has style type D while the autonymic variety has style type B. Perhaps it is an artifact of the poorly preserved nature of the material.

One collection, *Croat 57592,* from near Queremal in Valle Department, at 1300 m in an area of either *Premontane moist forest* or *Tropical Lower Montane wet forest,* may also represent this variety but has unribbed cataphylls. *Croat 57036,* a sterile collection from Cotopaxi Province, Ecuador, also has unribbed cataphylls and may represent the same taxon.

Philodendron rothschuhianum (Engl.) Croat & Grayum, Ann. Missouri Bot. Gard. 74: 659. 1987. *Syngonium rothschuhianum* Engl., in Engl. & K. Krause, Pflanzenr. IV. 23E (Heft 71): 124. 1920. TYPE: Nicaragua. Matagalpa: Matagalpa, 1000 m, 12°55′N, 85°55′W, *Rothschuh 229* (holotype, B). Figures 4, 9, 31, 336–340, 347, 348.

Hemiepiphytic to epiphytic or rarely terrestrial; stem appressed-climbing, creeping, sap watery, leaf scars conspicuous, 2 cm long, 2.5 cm wide; internodes short, semiglossy, 1.8–3 cm long, 1.5–3 cm diam., about as long as broad, gray-green, epidermis fissured; roots scurfy, few per node; cataphylls fleshy, soft, 16–23 cm long, unribbed then sharply 2-ribbed at apex, or bluntly 2-ribbed throughout or weakly 1-ribbed throughout, green, short dark striate, semiglossy, deciduous, emarginate with subapical apiculum at union of ribs at apex. LEAVES erect-spreading to spreading; **petioles** 33–71 cm long, 3–13(20) mm diam., subterete, moderately spongy, medium green, obtusely 1-ribbed near apex adaxially, surface weakly glossy, densely green striate; sheath inconspicuous; **blades** deeply 3-lobed, subcoriaceous, weakly bicolorous, gradually acuminate, long to very long acuminate at apex (the acumen inrolled, 1–2.5 mm long), ± hastate at base, 22–42 cm long, 25–57 cm wide (0.6–1 times longer than wide), (0.5–1 times the petiole length), about two-thirds as long as petiole, upper surface semiglossy, lower surface weakly glossy, slightly paler; sinus hippocrepiform; median lobes 16–39.5 cm long, 7–20 cm wide; lateral lobes narrowly ovate, 14–28 cm long, 5–17 cm wide, directed toward apex, broadly confluent 2–5 cm with medial lobe, the margins undulate; midrib sunken to narrowly concave, paler than surface above, almost round-raised, paler than surface below; basal veins 10–15 per side, the remainder arranged in a ± regular manner in the posterior lobe, coalesced in part throughout much of their length into a central rib; posterior rib usually not naked, sometimes naked for 1 cm, rarely to 2.5 cm; primary lateral veins 5–12 per side, departing midrib at a 50–65° angle, narrowly sunken, concolorous above, convex below; interprimary veins sunken and concolorous above, raised, almost as conspicuous as primary lateral veins below; minor veins darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2–3(9) per axil; peduncle 5.2–21 cm long, 5–10 mm diam., medium green, densely lineate; **spathe** (6.5)8–14(16) cm long, (0.6–2.2 times longer than peduncle), markedly constricted above the tube; spathe

blade pale green to greenish white to yellowish green outside, to ca. 5 cm wide when open, ca. 2.4 cm diam. at constriction, greenish white to creamy white inside; spathe tube ellipsoid, 4–7 cm long, pale green to yellowish green outside, greenish to greenish white to creamy white inside; **spadix** very short stipitate; somewhat protruding forward at anthesis, 10.5 cm long, constricted at base of fertile staminate portion; pistillate portion pale lime-green, 3.7 cm long in front, 2.5 cm long in back, 1–1.3 cm diam. at apex, 1.2–1.4 cm diam. at middle, 1.2 cm wide at base; staminate portion 6.4–9.3 cm long; fertile staminate portion creamy white, clavate, 1 cm diam. at base, 1.3 cm diam. at middle, 1 cm diam. ca. 1 cm from apex, usually broader than the pistillate portion; sterile staminate portion broader than fertile or pistillate portion, creamy white, 1.6–1.9 cm diam. at base, 1.3–1.4 cm. diam. at apex; pistils 1.6–2.6 cm long, 1.2 mm diam.; ovary 5–7-locular, 0.8 mm long, 1.1 mm diam., with sub-basal placentation; locules 0.8 mm long, 0.3–0.4 mm diam.; ovule sac 0.6 mm long; ovules 1 per locule, contained within translucent, gelatinous ovule sac, 0.3–0.5 mm long, longer than funicle; funicle 0.1–0.3 mm long (can be pulled free to base), style 0.6 mm long, 1.2 mm diam., similar to style type B; style apex sloping to rounded; stigma brush-like, hemispheroid, 0.7–1 mm diam., 0.3–0.6 mm high, covering entire style apex; apex drying button-like, with or without radial ridges from center; the androecium truncate, oblong, ± prismatic, margins irregularly 4–6-sided, 1–1.6 mm long, 1.5–1.9 mm diam. at apex; thecae oblong, 0.4 mm wide, ± parallel to one another, nearly contiguous; sterile staminate flowers blunt, sometimes clavate or prismatic or irregularly 5–6-sided or 3–6-sided, 1.7–2.3 mm long, 1.6 mm wide. Berries pale green or pale yellow-green to greenish white, 4 mm long, 2.5 mm diam.; seeds 1–3, medium green, (1.2)2.1–2.3 mm long, 0.6–0.8 mm diam., within thin envelope. JUVENILE plants with petioles sheathed to about midway; blades with posterior lobes hastate, acuminate at apex, promptly auriculate on posterior margin, broadly confluent with anterior margin on anterior margin.

Flowering in *Philodendron rothschuhianum* occurs during the dry season and early rainy season. Most collections have been made in March, but flowering occurs as late as August. Post-anthesis collections have been made from January through November (except October), but are particularly abundant from March through May. Immature fruiting collections have been made from April through September (also December), but mature fruits are known from only August.

Philodendron rothschuhianum ranges from Honduras (Gracias a Dios) and from Nicaragua (Río San Juan, Zelaya, Jinotega, and Matagalpa) to Panama (Bocas del Toro, Veraguas, and Coclé), principally on the Atlantic slope, from sea level to 1450 (mostly less than 1000) m elevation. It occurs in *Premontane wet forest, Tropical wet forest,* and less frequently in wetter parts of *Tropical wet forest* and *Premontane rain forest* life zones.

Philodendron rothschuhianum is a member of *P.* sect. *Tritomophyllum.* This species is distinguished by its short internodes; unribbed, deciduous cataphylls; subterete, moderately spongy petioles; and especially by its deeply three-lobed blades about two-thirds as long as the petioles with the lateral lobes broadly confluent with the medial lobe and the sinus hippocrepiform and naked along the posterior rib for a short distance from the petiole.

Philodendron rothschuhianum is most frequently confused with *P. tripartitum,* which differs in having less auriculate lateral lobes that are scarcely or not at all naked along the posterior rib. In addition, *P. tripartitum* has a much more slender, scarcely constricted, spathe tube reddish within (vs. a markedly inflated, uniformly greenish tube in *P. rothschuhianum*).

In terms of leaf shape, *P. rothschuhianum* is closest to *P. cotobrusense.* The latter differs in medial lobes with 18–19 pairs of primary lateral veins (vs. 5–12 pairs for *P. rothschuhianum*).

The style apex is apparently variable in this species, with *Croat 66772* and *Neill 1569* having type B styles while *Croat 35657* has style type D. The latter has the style apex prolonged into a distinct boss separated from the rest of the style apex by a distinct neck.

Additional specimens examined. COSTA RICA. **Alajuela**: Quebrada Guillermina, on N side of Volcán Arenal, 500 m, 10°29′N, 84°42′W, *Lent et al. 3415* (F, U); Naranjo–Aguas Zarcas, 8 km NE of Quesada, 600 m, *Croat 46942* (MO); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, ca. 850 m, *Croat 43567* (MO); *43637* (MO); Monteverde Biological Reserve, Río Peñas Blancas, 800 m, *Bello 1980* (CR, INB); 850–900 m, 10°20′N, 84°43′W, *Haber & Bello 6836* (MO); 850 m, 10°19′N, 84°43′W, *Haber & Cruz 8409* (MO); Finca de Tomás Guindon, 900 m, 10°19′N, 84°43′W, *Bello 763* (CR, MO); Río Sarapiquí, road to Colonia Virgen del Socorro, ca. 740 m, 10°5.5′N, 84°10.5′W, *Grayum & Hammel 5516* (B, CR, MO); ca. 800 m, *Burger & Antonio 11101* (CR, F); *11097* (F); 830 m, *Croat 68301* (MO); Vara Blanca–Puerto Viejo, 3 mi. N of San Miguel, 380 m, *Croat 35657* (CR, MO); Cañas–Upala, 3 km NNE of Bijagua, 450 m, 10°45′N, 85°3′W, *Burger & Baker 9881* (CR, F); 8 km N of Bijagua, 300 m, *Croat 36502* (CR, MO); 13.8 km N of Bijagua, 100–150 m, *Croat 36438* (MO); *36402* (CR, MO); near Río Zapote, 1.8–2.7 km S of Río Canalete, 100 m, *Croat 36402* (MO); 13 km W of Fortuna, Río Tabacón, 500–550 m, 10°29′N, 84°43′W, *Liesner et al. 15250* (MO); 15 km

NW of Arenal by air, 700 m, 10°34.5′N, 84°54′W, *Liesner et al. 15088* (MO); *15065* (MO); San Ramón, *Bittner & Venschott 1941* (CR); *Nilsson 460* (CR). **Cartago**: 4 km SE of Pejibaye, 700 m, 9°48′N, 83°42′W, *Liesner et al. 14330* (MO); Turrialba, *León 393* (US). **Guanacaste**: Parque Nacional Guanacaste Estación Pitilla, 600 m, 11°02′N, 85°25′18″W, *Hammel et al. 17372* (CR, MEXU, MO, NY, U, USJ). **Heredia**: near Tirimbina, E of Río Sarapiquí, 150–250 m, 10°24′N, 84°7′W, *Burger & Burger 8026* (F); Tirimbina, 700 ft., *Proctor 32148* (LL); La Selva Field Station, 100 m, *Jacobs 2826* (DUKE); *Folsom 9874* (DUKE); 50–80 m, 10°26′N, 84°01′W, *Grayum & Chavarria 8300* (MO); Puerto Viejo de Sarapiquí, *Grayum 2120* (DUKE); ca. 100 m, *Grayum 2856* (MO); *Croat 57199* (MO, voucher of live plant of *Grayum 2856*); Río Puerto Viejo, ca. 2 km upstream from confluence with Río Sarapiquí, 100 m, 10°26′N, 84°10′W, *Burger & Stolze 5756* (CR, US); Volcán Barva, Río Peje–Río Sardinalito, 700–950 m, 10°17.5′N, 84°04.5′W, *Grayum 6981* (CR, MO); 700–800 m, 10°17.5′N, 84°04.5′W, *6720* (CR, MO). **Limón**: ca. 1 mi. NE of Bribrí, ca. 40 mi. SW of Limón, above Río Catarata, 50–100 m, *Croat 43245* (MO); 7 km SW of Bribrí, 100–250 m, *Gómez et al. 20320* (MO); Río Pacuare, 50–100 m, 10°05′N, 83°29′W, *Burger & Liesner 6895* (F, MO); vic. of Guápiles, 300–500 m, *Standley 37469* (US); 2 km W of Río Toro Amarillo, W of Guápiles, 275 m, 10°13′N, 83°50′W, *Thompson & Rawlins 1216* (CM); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson et al. 7138* (RSA); Bahía de Portete Parque Nacional, 0–10 m, 10°N, 83°05′W, *Thompson & Rawlins 1176* (CM); Cerro Coronel, E of Río Zapote, along and above new road, within 1 km of Río Colorado, 10–40 m, 10°40′N, 83°40′W, *Stevens 24277* (CR, MO); E of Río Zapote, 10–100 m, 10°40′N, 84°40′W, *Stevens 23974* (CR, MO); E of Laguna Danto, 20–170 m, 10°41′N, 83°38′W, *Stevens 24453* (CR, MO); Parque Nacional Tortuguero, Puesto Cuatro Esquinas, 4 m, 10°32′N, 83°30′W, *Robles 1837* (CR, MO); Barra del Colorado, 0–2 m, 10°47′N, 83°35′W, *Stevens 24073* (CR, MO); Río Colorado, Barra del Colorado, 1–5 m, 10°47′40″N, 83°35′30″W, *Davidse & Herrera 30869* (MO); 2 airline km SSE of Islas Buena Vista, 10–120 m, 10°40′N, 83°40′W, *Davidse & Herrera 31035* (MO); Río Reventazón, Finca Montecristo, below Cairo, ca. 25 m, *Standley & Valerio 49027* (US); Parque La Amistad, Fila Tsiurábeta, between Río Urén and Río Lari, 800 m, 9°27′30″N, 83°W, *A. Chacón 294* (CR, MO). **Puntarenas**: hills above Santa Elena, 3 km N of Monteverde, 1450 m, 10°20′N, 84°50′W, *Haber & Bello 5067* (MO). **San José**: S of San José, *Greenman & Greenman 5353* (MO); Braulio Carrillo National Park, Fila Carrillo, 700 m, *Gómez et al. 21149* (CR, MO); 600–700 m, *Croat 78777* (CR, INB). HONDURAS. **Gracias a Díos**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9146* (CM, MO, NY, UNAH). NICARAGUA. **Chontales**: Cerro Buenavista, 5 km N of Cuapa, *Neill 637* (MO); 4 km NW of Santo Domingo, 280 m, ca. 12°17′N, 85°06′W, *Grijalva et al. 3771* (MO). **Jinotega**: Finca San Luis, 21 km from Valle del Cuá, NW de El Cedro, 700 m, 13°30′N, 85°38′W, *Moreno 959* (MO); Río Bocay, Caño Litutus, ca. 175 m, ca. 13°58′N, 85°21′W, *Stevens et al. 16617* (MO); Salto Kayaska, 190–340 m, ca. 13°51′N, 85°22′W, *Stevens et al. 16484* (F, MO). **Matagalpa**: Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradón, slopes NW of Hacienda San Sebastián, 800–1100 m, 13°14–15′N, 85°38′W, *Stevens 21258* (MO); summit of El Toma Road, *Neill 1569* (HNMN, MO); 10.5 km NW of Matagalpa, ca. 1000 m, 12°57′N, 85°51′W, *Moreno 10233* (MO); El Paraíso, 10 km de Matagalpa, 800–820 m, 12°59′N, 85°51′W, *Moreno 6607* (MO); N of Cerro Musún, near Wanawás, *Araquistain & Moreno 2741* (LE, MO); NW of Cerro Musún, near Paylo, 500–800 m, *Araquistain & Moreno 2572* (MO); 800–1200 m, *2510* (MO); *2495* (CAS, HNMN, MO); 300–600 m, *2471A* (MO); Río Bilampí, NW of Cerro Musún, 4 km SW of Wanawás, 200–500 m, 13°00–01′N, 85°14′W, *Araquistain & Moreno 2614* (HNMN, MO, US); Comerca Wanawás, 180–200 m, 12°02–03′N, 85°13′W, *Araquistain & Moreno 2398* (HNMN, K, MO); near Cerro Musún, 8 km from Población Wanawás, Palán Grandre, 500–800 m, 12°59′–13°N, 85°14′W, *Araquistain & Moreno 2355* (HNMN, MO, NY); Río Bilampí Valley, Cerro Musún, Salto Grande of Quebrada Negra, 500–800 m, *Neill 1800* (MO). **Río San Juan**: Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed), 200 m, *Neill 3367* (MO); *Neill & Vincelli 3541* (BM, MO); Río Indio Valley, 6 km upstream from the junction with Caño La Pimienta, 300–600 m, *Neill 1557* (MO); Río Sábalo, Buenos Aires, 70 m, 11°02′N, 84°28′W, *Moreno 25595* (MO). **Zelaya**: ca. 1.5 km NE of Las Esperanza de Las Quebradas, 300–350 m, ca. 13°38′N, 85°02′W, *Stevens & Moreno 19308* (MO); Limbaika–El Empalme, ca. 3.9 km SE of El Empalme, ca. 65 m, ca. 13°39′N, 84°24′W, *Stevens 12930* (MO); road to Mina Nueva América, ca. 10 km from main road, *Stevens 12687* (MO); Rosita–Puerto Cabezas, ca. 15.7 km SW of Río Kukalaya, <100 m, ca. 13°58′N, 84°12′W, *Stevens 8500* (MO); Cerro El Inocente, near Caño Majagua, ca. 800–1000 m, ca. 13°45′N, 85°W, *Stevens 6805* (MO); Siuna–Matagalpa, ca. 31.4 km beyond Río Uli, ca. 8.9 km beyond Rosa Grande La Balsama, <200 m, *Stevens 7456* (MO); Cerro Saslaya–San José del Hormiguero, from Loma Mollejones eastward, ca. 200–400 m, ca. 13°44–45′N, 84°57–58′W, *Stevens 7049* (BM, MO); Caño Majagua, ca. 750–850 m, ca. 13°45′N, 85°00–01′W, *Stevens 6936* (MO); Caño Majagua–Caño Sucio, ca. 600–800 m, ca. 13°45′N, 84°59′–85°W, *Stevens 6821* (MO, PMA); vic. of La Pimienta, ca. 13°45′N, 84°59′W, *Pipoly 6225* (MO); Cerro La Pimienta–El Hormiguero, ca. 800–1000 m, ca. 13°45′N, 84°59′W, *Pipoly 6012* (MO); Cerro La Pimienta, number 1, ca. 900–980 m, ca. 13°45′N, 84°59′W, *Pipoly 5129* (MO); ca. 13 km above Kururia, on road to San Jerónimo, <200 m, *Pipoly 3794* (MO); Risco de Oro, ca. 40 m, *Pipoly 5043* (MO); 10 km NE of Siuna, along Caño Madriguera, 250 m, *Neill 3754* (BM, MO); 4 km NE of Siuna, road to El Dos, 300 m, 13°45′N, 84°45′W, *Moreno & Robleto 20856* (MO); 1 km W of El Naranjo, 200–210 m, 13°34′N, 85°11′W, *Moreno & Robleto 20616* (MO, QCA); SE of Cerro El Hormiguero, ca. 900–1000 m, 13°44′10″N, 84°59′50″W, *Grijalva 473* (MO); Río Iyas, Quebrada El Toro, 260–280 m, *Vincelli 370* (MO); near San Juan del Norte, *C. Smith 5* (F). PANAMA. **Bocas del Toro**: Gualaca–Chiriquí Grande, ca. 10 km SW of Chiriquí Grande, ca. 300 m, 8°52′N, 82°10′W, *Thompson 4936* (CM); 4.2 mi. S of Chiriquí Grande, ca. 0 m, 8°55′N, 82°09′W, *Croat 66815* (MO); Fortuna Lake area, Continental Divide, 900 m, 8°48′04″N, 82°15′04″W, *McPherson & Aranda 10185* (MO, PMA, W); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60276* (CM, MO, RSA); 850–950 m, 8°40′04″N, 79°50′04″W, *McPherson 10546* (AAU, M, MEXU, MO, US); ca. 300 m, ca. 8°50′N, 82°15′W, *McPherson 8522* (K, MO, US); 6.6 mi. N of bridge over Fortuna Lake, 780 m, 8°45′N, 82°18′W,

Croat 66772 (MO); 1.2 mi. N of Divide, 910 m, 8°44′N, 82°17′W, *Croat 60462* (MO, PMA); 1.6 mi. N of Divide, 850 m, 8°48′N, 82°13′W, *Croat 74931* (MO); 1.6 mi. N of Divide, 770 m, 8°45′N, 82°17′W, *Croat & Zhu 76534* (MO); Río Cricamola, Finca St. Louis–Konkintoë, ca. 10–50 m, *Woodson et al. 1919* (MO). **Coclé**: El Copé region, 4.5 mi. N of El Copé, 750 m, 8°38′N, 80°35′W, *Thompson 4760* (CM, MO); 5–6 mi. N of El Copé, 600–800 m, 8°38′N, 8°35′W, *Croat & Zhu 77224* (CM, MO); 680–770 m, 8°39′N, 80°36′W, *Croat 74828* (CM, MO); Alto Calvario, *Croat 68848* (MO). **Veraguas**: 15.6 km NW of Santa Fe, 450–550 m, *Croat 27704* (MO); 350–400 m, *27385* (MO).

Philodendron sagittifolium Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1849: 17. 1849. TYPE: Mexico. Veracruz: Río Nautla at Pital, Apr. 1841, *Liebmann s.n.* (holotype, C). Figures 346, 350–356.

Philodendron daemonum Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1849: 17. 1849. TYPE: Mexico. Veracruz: vic. Colipa at Potrero de Consoquitla, *Liebmann s.n.* (holotype, C; isotype, K).

Philodendron tanyphyllum Schott, Prod. Syst. Aroid.: 272. 1856. TYPE: Mexico. *Liebmann s.n.* (W destroyed). Schott's ic. 2557 (neotype, here designated, W).

Philodendron sanguineum Regel, Ind. Sem. Hort. Petrop. 82. 1868. TYPE: Mexico. Locality unknown: *Karwinsky s.n.* (holotype, LE? no longer extant); t. 621 in Regel, Gartenflora 18. 1869 (neotype, here designated).

Philodendron lancigerum Standl. & L. O. Williams, Ceiba 1. 232. 1951. TYPE: Costa Rica. Puntarenas: vic. Palmar Norte, Río Térraba, 30 m, *Allen 5612* (holotype, US). Costa Rica. Puntarenas: along road between Chacarita and Rincón de Osa, ca. 6 km W of Interamerican Highway at Chacarita, 160 m, ca. 8°45′N, 83°18′W, *Croat & Grayum 59728* (epitype, here designated, MO–3319112; isoepitypes, B, CR, F, K, NY, PMA, US).

Philodendron tuxtlanum G. S. Bunting, Gentes Herb. 9. 353. 1965. TYPE: Mexico. Veracruz: vic. Santiago Tuxtla, *Bunting & Davies 162* (holotype, US).

Usually hemiepiphytic, rarely terrestrial or epilithic; stem appressed-climbing, parchment-white, sap turning blackish, slimy; internodes usually terete, weakly angular, sometimes obscurely flattened on one side or closely and acutely ribbed, semiglossy to matte, 1–20 cm long, 1.5–4 cm diam., dark green, becoming usually gray-green to brown, sometimes pale yellow-green, epidermis somewhat ridged ("wrinkled"), sometimes fissured transversely; roots reddish brown, 6–10 mm long, 3–5 mm diam., arising from and along the node on one side; cataphylls 18–39 cm long, usually weakly 1-ribbed, sometimes unribbed or weakly to sharply 2-ribbed or sharply 1-ribbed (ribs to 1 cm high), soft, green, sometimes reddish to pinkish, sometimes sparsely green-spotted, purple-maroon or darker striate near base, drying reddish brown, margins sometimes prominently and thinly raised, usually soon deciduous, rarely persisting as a rotting mass, rounded at apex; **petioles** 20–65(91) cm long, 3–15 mm diam., usually subterete, moderately spongy to firm, medium green, drying greenish brown, obtusely flattened, usually obtusely and narrowly sulcate, rarely obtusely and broadly sulcate adaxially, surface minutely and densely short purple- or occasionally white-striate, sometimes dark green or violet-purple blotched, sometimes smooth to irregularly ribbed and folded; sheath subtending an inflorescence, 5–8 cm long; **blades** ovate to ovate-triangular, semiglossy, moderately coriaceous, weakly to moderately bicolorous, acuminate to narrowly acuminate, sometimes short-acuminate at apex, prominently cordate to ± sagittate at base, 30–72 cm long, 15–39 cm wide (1.85–2 times longer than wide), (0.6–1.6 times longer than petiole), margins somewhat hyaline, weakly revolute, upper surface medium green, drying brownish green to greenish brown, semiglossy, lower surface pale yellow-green, sometimes reddish, drying usually reddish brown, sometimes yellowish brown, weakly glossy to matte; anterior lobe 24–61 cm long, 13–34.5 cm wide (2–5.1(5.5–6.4) times longer than posterior lobes); posterior lobes usually narrowly rounded, 6–20.5 cm long, 5–17.6 cm wide; sinus ± V-shaped to almost closed, 6–15 cm deep; midrib flat to weakly raised, paler than surface, drying broadly raised and ± concolorous above, convex to narrowly raised, sometimes maroon-spotted or with white flecks, concolorous to darker than surface, drying broadly raised and reddish below; basal veins 3–5(6) per side, with 0–1(2) free to base, third and higher order veins sometimes coalesced 2.5–4.5 cm, a few additional veins sometimes coalesced to 6.5 cm; posterior rib not at all naked or only briefly so; primary lateral veins 4–9 per side, departing midrib at a 60–70° angle, weakly curved to the margins, but usually turned prominently up just before the margin, rather prominently downturned just before the midrib, round-raised to flat to obtusely sunken and paler than surface above, convex, concolorous to darker than surface below; interprimary veins weakly sunken, concolorous above, flat, darker than surface below; minor veins weakly visible below, arising from both the midrib and primary lateral veins, drying moderately prominent, weakly undulate, alternating with dark, mostly contiguous secretory ducts. INFLORESCENCES erect, 1–3 per axil; peduncle 4–15 cm long, 1.6–1.8 cm diam., somewhat flattened to terete, green, sometimes tinged reddish, drying greenish, densely short and broad striate; **spathe** 8–22 cm long, 2–3 cm diam. (0.8–2.2 times longer than peduncle), weakly to obscurely constricted above the tube, semiglossy, usually green, sometimes

plum-red, often purple-spotted, densely short pale lineate throughout, weakly so near apex, blunt to narrowly cuspidate-acuminate to prominently acuminate, frequently tinged purplish violet at base; spathe blade green to pale yellow-green, 8–11 cm long (opening 3–4.3 cm wide, sometimes opening to near the base), greenish white, weakly tinged red-purple in throat to pale yellow-green or white inside, sometimes reddish throughout in age; resin canals appearing as continuous lines, red-purple to orange in color; spathe tube green, sometimes moderately to heavily tinged red-purple to red (B & K red-purple 3/7.5), with sparse, dark purplish spots (mostly medially) throughout outside, 4–7 cm long, 2.5–3.5 cm diam., red to reddish purple (B & K red-purple 3/7.5), white striate inside; **spadix** stipitate to 7 mm long; tapered toward apex, (8)9–16 cm long, broadest below the middle or near the base, usually protruding somewhat forward at anthesis but not curved; pistillate portion pale green (anthesis) to greenish white to yellow-green (post-anthesis), uniformly wide throughout or weakly tapered toward both ends, 2.5–6.2 cm long in front, 2–4.7 cm long in back, 1–1.2 cm diam. at apex, 1.1–1.7(2.1) cm diam. at middle, 1.1–1.7 cm wide at base; staminate portion 6.3–10.3(13) cm long; fertile staminate portion usually creamy white, sometimes pale green to pinkish, 9–13 mm diam. at base, 11–13 mm diam. at middle, 8–10 mm diam. ca. 1 cm from apex, broadest at base or middle, about as broad as the pistillate and sterile portions; sterile staminate portion often broader than the pistillate portion, white, (0.9–1)1.2–1.9 cm diam.; pistils (0.9)1.8–4.4 mm long, (0.9)1.3–2.3 mm diam.; ovary 6–9-locular, 1–1.7(3) mm long, 1.3–2.3 mm diam., with sub-basal placentation; locules 1–1.7(3) mm long, 0.2–0.4 mm diam.; ovule sac (0.6)0.8–1.2 mm long; ovules usually 2–4, rarely 5–8 per locule, 1-seriate (2-seriate, if 4 or more ovules), usually contained within translucent, gelatinous ovule sac, sometimes contained within gelatinous matrix (no true envelope), 0.1–0.5 mm long, usually longer than funicle; funicle 0.1–0.3 mm long (can be pulled free to base), sometimes adnate to lower part of partition, style (0.4)0.6–0.8 mm long, (0.8)1.2–1.6 mm diam., similar to style type B; style apex flat to sloping; stigma discoid or subdiscoid, truncate, (0.7)1–1.5 mm diam., (0.1)0.3–0.5 mm high, covering entire style apex, sometimes shallowly depressed at middle; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided to weakly ovate, ca. 1 mm long, 1.6–2 mm diam. at apex; thecae oblong, 0.4–0.6 mm wide, ± parallel to one another, sometimes contiguous; sterile staminate flowers blunt, irregularly 4–6-sided, sometimes clavate or prismatic, 1.4–2.1 mm long, 1.4–2 mm wide. INFRUCTESCENCE pink, green at base with reddish spots outside; berries pale yellowish, rarely orange, with stigmas reddish brown, 7 mm long; seeds 2–3 per locule, drying pale brown to tannish brown, narrowly ellipsoid to oblong-ellipsoid, 1.4–2 mm long, 0.7–0.9 mm diam., with faint striations.

Flowering in *Philodendron sagittifolium* occurs almost throughout the year, principally after the onset of the dry season and continuing throughout much of the rainy season. There is a slight geographical shift, with flowering beginning about one month earlier in Mexico and Guatemala (January through August, less frequently in September and October) and continuing somewhat longer in Panama (February through September, but also rarely in December). Fruits apparently mature in about two months' time, but mature fruits have seldom been collected, only from January and July.

Philodendron sagittifolium ranges from Mexico (Veracruz) to Colombia (and probably also to Venezuela), from sea level to 1800 m elevation. It is probably the most morphologically variable, and one of the most ecologically versatile, species in Central America. In Mexico, this species occurs in "Selva Alta Perennifolia," "Selva Mediana Subperennifolia," "Selva Baja Caducifolia," and "Bosque Caducifolio." In the remainder of Central America, it occurs principally in *Tropical moist forest* and *Premontane wet forest* but also in *Premontane rain forest* and *Tropical wet forest* life zones.

Philodendron sagittifolium is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species, though highly variable in most regards, can be characterized by its appressed-climbing habit; short, stout internodes; sharply two-ribbed, deciduous cataphylls; obtusely flattened, firm petioles usually spotted with violet-purple; and ovate-triangular, moderately coriaceous blades with the posterior rib not at all or only briefly naked along the sinus. Also characteristic is the externally green, frequently purple-spotted spathe, which is reddish purple on the tube within.

In Mexico and Guatemala, *Philodendron sagittifolium* is most easily confused with *P. advena* and *P. purulhense*, differing from both in having the blades somewhat triangular and drying reddish brown rather than generally ovate and drying blackened. See *P. advena* for additional discussion.

In Panama, *P. sagittifolium* may sometimes be confused with *P. annulatum*, which differs in having the petioles somewhat spongy with a purple distal ring, blades typically ovate-oblong, and spathes commonly white on the blade portion. It can be

confused at some stages of development with sterile specimens of *P. bakeri.*

Considering the highly variable nature of this species there are many noteworthy collections, only a few of which can be discussed here.

Whitefoord & Eddy 222 from Panama has the lower blade surfaces drying yellowish brown rather than reddish brown and spathe solid plum-red outside. Also noteworthy is *Hammel et al. 14598,* which reports fruit color to be orange.

A few collections from Puntarenas Province, Costa Rica (*Croat 57243, 67697, Grayum & Hammel 10066*), differ in having the primary lateral veins paler, rather than darker on the lower surface. Sterile specimens from Cocos island (*W. Klawe s.n., Foster 4177*) differ in having the minor veins minutely raised on the upper surface. These specimens may prove to represent distinct species.

A large number of sterile and ostensibly juvenile collections from Nicaragua are of uncertain identity. One series, including *Pipoly 3826, 4055, 5144, Stevens 7628, 12673, 12739,* may ultimately prove to be *P. bakeri.* Two other collections (*Pipoly 5190, 5194*) might prove to be still another species.

Croat 60804, from the coastal cordillera of Venezuela, reported as *P.* cf. *sagittifolium* (Croat & Lambert, 1986) is either this species or a very close relative.

When Regel described *P. sanguineum* Regel, he cited no specimens or country of origin, but Krause (1913) cited a collection he had prepared from the Berlin Botanical Garden of a cultivated Karwinsky collection from Córdoba in Veracruz State, Mexico. While no such collection still exists, Karwinsky collected in Mexico only a few years (1840–1843) before Regel described *P. sanguineum.* Thus it is possible that both Regel and Engler could have been dealing with the same material originally collected by Karwinsky at Córdoba.

Another synonym that deserves mention is *P. lancigerum* Standl. & L. O. Williams, corresponding to a narrow-leaved form of *P. sagittifolium* restricted to the Pacific lowlands of Costa Rica. Epitypification was necessary because the type specimen (*Allen 5612*) consists of only an inflorescence.

Additional specimens examined. BELIZE. **Cayo**: Mountain Pine Ridge, *Bartlett 13052* (MICH); Blancaneaux Lodge, *Wiley 460* (MO); Water Hole, near Vaca, *Gentle 2447* (MICH); Río Ma Cal, San Luis–Cuevas, 1050 ft., *Croat 23497* (MO); 1050 ft., *23539* (MO). **Toledo**: Punta Gorda, *Cosminsky 227* (F); Richardson Creek, lower part, affluent of Bladen Branch, lower part of Maya Mountains, 100–250 m, 88°46–48′W, 16°33′N, *Davidse & Brant 32334* (MO); Columbia road, *Gentle 6118* (LL); San Antonio, *Gentle 5510* (LL); Punta Gorda, *Cosminsky 226* (F); Columbia River Forest Reserve, SW Maya Mountains, trail between Gloria Camp and Edwards Camp to the S, 16°22′N, 89°10′W, *Holst 4499* (MO). COSTA RICA. **Alajuela**: 3 mi. N of San Miguel, 380 m, *Croat 35642* (CR, MO); 8.9 mi. NW of San Ramón, 1100 m, 10°10′30″N, 84°30′W, *Croat 68070* (L, MO); Río Sarapiquí, road to Colonia Virgen del Socorro, 830 m, 10°1′6N, 84°11′W, *Croat 68338* (MO). **Cartago**: Tapantí, ca. 1350 m, 9°47′N, 83°47.5′W, *Grayum 3890* (MO); 1400 m, 9°47′N, 83°48′W, *3322* (K, MO); 31 km S of Siquirres, 850 m, 9°57′N, 83°36′W, *Thompson & Rawlins 1159* (CM); *1160* (CM); 7 km W of Turrialba, *Croat 36829* (MO); Turrialba, Moravia de Chirripó, 1200 m, *Campos & Chavarría 40* (CR, INB); Río Pejibaye, 2 km SW of Taus, 750 m, 9°29′N, 83°41′W, *Lent 2967* (CR, F). **Heredia**: La Selva Field Station, *Hammel 10244* (MO); *Grayum 2306* (MO); *Hammel 9641* (DUKE); La Zona Protectora, SSE of Magsasay, *Schatz 722* (CR, DUKE, MO); 4 mi. N of Vara Blanca, 1350 m, *Croat 35579* (MO). **Limón**: vic. of Moín, 0 m, 10N, 83.04W, *Croat 61206* (MO); Parque Nacional Tortuguero, 2 km S of Tortuguero, 3 m, 10°31′N, 83°30′W, *Robles 2166* (CR, MO); *2178* (CR, MO). **Puntarenas**: Palmar Sur–Piedras Blancas, 20 m, *Croat 32917* (MO); Quebrada Aparicio–Quebrada Aguabuena, Rincón de Osa, 200–400 m, 8°42′N, 83°31′W, *Grayum et al. 4017* (CR, MO); Rincón de Osa, region to W of airstrip, 40–100 m, *Utley & Utley 1119* (F); San Vito de Coto Brus–Ciudad Neily, 300–600 m, 8°41′N, 82°56.5′W, *Hammel 14159* (CR, MO); El Campo, Aguabena, 350 m, 8°42′50″N, 83°31′42″W, *Herrera 3959* (INB, MO); Las Brisas–Las Juntas de Coto Brus, ca. 900 m, 8°52′N, 82°57′W, *Grayum & Hammel 5692* (INB, MO); Parque Nacional Corcovado, Sirena, 1–10 m, 8°28′N, 83°35′W, *Kernan & Phillips 1028* (MO); 1–50 m, *Kernan & Phillips 1089* (MO); *Kernan 461* (CR, MO), *574* (CR, MO); 10 m, *Aguilar 3396* (INB); Río Claro, 5 m, *Kernan 783* (CR, MO); Las Cruces Botanical Garden–Río Jaba, ca. 3 km SW of San Vito de Coto Brus, ca. 1050–1200 m, 8°47′N, 82°58′W, *Grayum 5624* (CM, CR, INB, MEXU, MO, U); San Vito de Java, ca. 4000 ft., *Croat 32904* (MO); 1 mi. S of San Vito de Java, ca. 3500 ft., *Raven 21882* (BM, DS, F); 6 km S of San Vito de Java, 4000 ft., *Raven 22009* (DS, F, WIS); Las Cruces Botanical Garden, ca. 1300 m, *Croat 44440* (MO); Golfito, near TV transmission tower, 2000 ft., 8°49′N, 82°58′W, *Croat 57243* (MO), *57231* (MO); Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1150 m, *Croat 22287* (F, MO), *22257* (MO); hills above Palmar Norte, 100–200 m, *Croat 35141* (MO); Punta Catedral, ca. 7 km SE of Quepos, 20–70 m, 9°22.5′N, 84°09′W, *Grayum & Sleeper 5903* (MO); Punta Quepos (3 km S of Puerto Quepos), 0 m, 9°24′N, 84°10′W, *Grayum 6613* (CR, MO, PMA, US); road to Rincón de Osa, 16.5 km W of Inter-American Highway, 280 m, 8°45′N, 83°22′W, *Grayum et al. 7550* (INB, MO); Reserva Forestal Golfo Dulce, S of Rincón de Osa, 150 m, 8°37′N, 83°28′W, *Hammel & Robles 16728* (CR, MO); 150–200 m, *16759* (CR, MO); 450 m, *G. Herrera 3953* (CR, INB); ca. 0.7 km N of Golfito–Villa Briceño road, 160–260 m, 8°40′30″N, 83°12′W, *Grayum & Hammel 10066* (CR, MO); Cantón de Golfito, Jiménez, Alto de la Carbonera, road to Cerro de Osa, 200–350 m, 8°25′30″N, 83°19′W, *A. Chacón 1069* (CR, INB, MO); 3.1 mi. NW of center of Golfito, 30 m, 8°11′N, 83°12′W, *Croat 67632* (CM, CR, MEXU, MO, WIS); Piedras Blancas–Rincón Road, Mile 3.7, 90–105 m, *Croat 67697* (CR, MO); Cocos Island, valley behind Bahía Iglesias, *Foster 4177* (F, MO); *Klawe s.n.* (POM). **San José**: San Isidro de El General–Dominical, SW of San Isidro,

4.8 mi. from Río Pacuare, 1000 m, *Croat 35254* (MO); 9 mi. SW of Río Pacuare, 680 m, *35343* (MO); ca. 0.5 mi. above turnoff to Canaán at Rivas, 900 m, *Croat 43430* (CR, MO); *43415* (MO); Estación Carrillo, Fila Cañon del Río Sucio 450–700 m, *A. Chacón & Herrera 1705* (CR, MO); Carara–El Sur de Turrubares, 200–310 m, 9°45′15″N, 84°31′30″W, *Grayum 10451* (CR, INB, MO); Z. P. La Cangreja, Santa Rosa de puriscal, 400 m, 9°42′50″N, 84°23′30″W, *Morales 1468* (CR, MO); Acosta, Valle del Candelaria, 1000–1050 m, *Morales & González 4581* (CR, INB); Tarrazu, vic. Hormiguero, 1100–1200 m, *Croat 78938* (INB, MO); *78959* (CR, INB, MO); 990–1100 m, *Croat & Hannon 79110* (MO); Parque Nacional, sector Esquinas, vic. Fila Gamba, 200–300 m, *Croat & Hannon 79294* (INB, MO). GUATEMALA. Eastern portions of Verapaz and Chiquimula, *Watson 106* (GH). **Alta Verapaz**: E of Tactic, 1300 m, *Steyermark 43993* (F, US); near Chirriacté, on the Petén Highway, ca. 900 m, *Standley 92189* (F); Chapultepec Farm, 62 km from Cobán on Sebol Road, *Contreras 4823* (LL); Río Carchá, Cobán–San Pedro Carchá, ca. 1360 m, *Standley 89891* (F). **Baja Verapaz**: Mpio. Purulhá, El Progreso–Cobán, Hwy. CA-14, 17 mi. N of junction with Hwy. 17, 1620–1720 m, 15°13′N, 90°12′W, *Croat & Hannon 63766* (CAS, CR, EAP, MO, SAR, USCG). **Chimaltenango**: Quisaché, 1800 m, *Standley 62029* (F). **Izabal**: Escobas–Santo Tomás, Santo Tomás Bay, 0–2 m, *Steyermark 39331* (F); between Milla 49.5 and ridge 6 mi. from Izabal, Montaña del Mico, 65–600 m, *Steyermark 38506* (F, US); vic. EXMIBAL Camp 2 (La Gloria), NW of Lake Izabal, 400–500 m, *Jones & Facey 3283* (NY); Sierra de las Minas, 13 km E of Doña María, 240 m, ca. 15°14′N, 89°20′W, *Harmon & Fuentes 5857* (UMO); Río Frío, 75–150 m, *Steyermark 41533* (F, LL). **Petén**: Canchacan, near San Luis, *Lundell 16325* (LL); Dolores, 300 m, *Contreras 2562* (LL). **Quezaltenango**: La Shuya, SW of San Martín Chile Verde, ca. 1620 m, *Standley 67882* (F). HONDURAS. Mont. de la Flor., 3300 ft., *von Hagen & von Hagen 1304* (F, NY). **Atlántida**: Quebrada Grande, ca. 10 km SW of La Ceiba, 80–200 m, 15°42′N, 86°51′W, *Liesner & Mejía 26011* (MO); *26352* (MO); 80–180 m, 15°42′N, 86°51′W, *Liesner 26179* (MO). **Comayagua**: El Achote, above Siguatepeque, 1350 m, *Yuncker et al. 5894* (F, GH, K, MO, NY, U). **El Paraiso**: El Junquillo–El Robledal, Sierra el Chile, 1300 m, *Molina 14142* (EAP, F, NY). **Olancho**: Catacamas–La Presa, N of Catacamas, 500–600 m, *Standley 18698* (EAP); *Nelson 9875* (TEFH, US); Río Olancho, San Esteban–Bonito Oriental, 14.8 mi. NE of San Esteban, 635 m, 15°25′N, 85°47′W, *Croat & Hannon 64405* (DUKE, LL, MO); San Francisco de la Paz–Gualaco, 7.3 mi. NE of San Francisco de la Paz, 1130 m, 14°58′N, 86°12′W, *Croat & Hannon 64197* (B, BM, CM, MICH, MO, NY, QCA); 13.6 mi. SW of Gualaco, 1300 m, 15°N, 86°07′W, *Croat & Hannon 64295* (F, K, MO, NY); Mpio. La Unión, 6 mi. E of La Unión along road to Olanchito, 950 m, 15°03′N, 86°35′W, *Davidse et al. 35428* (MO). **Yoro**: Cordillera Nombre de Dios, El Guaymon–San José de Texíguat, Cerro Aguacatales, 830 m, 15°29′N, 87°37′W, *Davidse et al. 34524* (EAD, MO, TEFM); *34524* (EAD, MO, TEFM); Río Pijol Valley, 6–7 km S of Nueva Esperanza, 1570–1670 m, 15°12′N, 87°35′W, *Liesner 26581* (MO). MEXICO. Patria, *Engler 198* (GH, P). **Chiapas**: Mpio. Ocosingo, 16 km NW of Boca Lacantún, 900 m, *Martínez 21345* (MEXU, MO); 12 km N of Monte Líbano, 950 m, *Martínez 21252* (MEXU, MO); Cascada Corralita, SW of Ocosingo, 600 m, 16°59′N, 92°08′W, *Hammel et al. 15677* (MO); Palenque–Bonampak, 69 mi. SW of Palenque, 450 m, *Croat 40197* (F, MO), 6 mi. N of Ocozocoautla, 1000 m, *Croat 40581* (B, MEXU, MO); Palenque–Ocosingo, Hwy. 199, 43 mi. SW of Palenque, 810 m, *Croat 40337* (MO); 13 mi. N of Ocozocoautla, 900 m, *Croat 40632* (MO); San Cristóbal de Las Casas–Palenque, Villa Paraíso, 136 km NE of San Cristóbal, 450 m, 17°29′N, 92°05′W, *Hammel et al. 15641* (MO); 18–20 km N of Ocozocoautla, 800 m, *Breedlove 25202* (DS); 3 mi. N of Pueblo Nuevo Solistahuacán, 1700 m, *Breedlove & Smith 32436* (DS); 6700 ft., *Thorne & Lathrop 40267* (RSA). **Morelos**: Cuernavaca, Barranca del Salto de San Antonio, *Moore & Bunting 8823* (BH); Iturbide, *Bourgeau 1417* (K, P). **Oaxaca**: Latani, Dtto. Choapam, 900 m, 17°24′N, 95°48′W, *Schultes & Reko 900* (ECON, GH); Sierra de Juárez, Tuxtepec–Oaxaca, Highway 67, 6–14 mi. above bridge at Valle Nacional, ca. 580 m, *Moore & Bunting 8902* (BH, CM); *8892* (BH); 660 m, *Croat 39752* (MO); *39757* (MO); *43917* (CM, MO); 1400 m, *Croat 48000* (L, MEXU, MO); 705 m, 17°44′N, 96°19′W, *Croat & Hannon 65537* (B, MO); 55 km S of Tuxtepec, 630 m, 17°37′N, 96°20′ W, *Hammel & Merello 15482* (MO, NY); Uxpanapa region, Esmeralda–Río Verde, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63237* (CR, MO, VEN); *63299* (MO); Palomares–Matías Romero, road to Uxpanapa, 44 km E of entrance at Sarabia, on Rte. 185, 125 m, 17°09′N, 94°37′W, *Hammel & Merello 15556* (MO); *15555* (MO); Uxpanapa, 14 km E of Campamento La Laguna (Poblado D.S.), 150 m, 17°05′N, 94°35′W, *Hammel & Merello 15578* (MO); Río Uxpanapa, *Matuda 38666* (MEXU); Ixtlán, Mpio. Comaltepec, Puerto Antonio, ca. 1300 m, 17°45′N, 96°30′W, *Luna 436* (MO); Highway 175, 1 km above Vista Hermosa, 1255 m, 17°35′N, 96°21′W, *Boyle & Boyle 684* (MO). **Veracruz**: Conejo–Huatusco, Hacienda El Mirador vicinity, km 45 on highway, *Moore & Bunting 8862* (BH, MO); *8863* (BH, MO); El Mirador, *8857* (BH, MO); Fortín de las Flores (Posada Loma), 850 m, *Nevling & Gómez-Pompa 287* (cultivated, XAL); Catemaco–Acayucan, ca. 8 mi. S of Catemaco, near Zapoapan, ca. 400 m, *Moore & Bunting 8925* (BH); Fortín, Cervecería Moctezuma, 1000–1150 m, *Croat 39415* (CM, F, MO); 900 m, *Croat 44038* (MO); 5.7–6 mi. from Catemaco, road to Sontecomapan, ca. 380 m, *Moore & Bunting 8941* (BH); Playa Montepío, 0 m, 18°38′N, 95°05′W, *Hammel & Merello 15498* (BR, CM, MO); Coatzacoalcos River, Fortuño, 30–50 m, *Williams 8702* (F); Estación de Biología Trioucak "Los Tuxtlas," ca. 31 km by road N of Catemaco, along road to Montepío, 250–300 m, 18°60′N, 95°07′W, *Grayum & Sleeper 8355* (MO); 300 m, 18°44′N, 85°10′W, *Hammel & Merello 15490* (CM, MO); 170–200 m, *Gentry et al. 32488* (MO); 250 m, *Ibarra 589* (MO); Mpio. Coatepec, Tuzamapan–Jalcomulco, Cerro de Achichuca, 700 m, 19°23′N, 96°48′W, *Castillo & Tapia 678* (F, MO); Mpio. Hidalgotitlán, toward La Laguna, 160 m, 17°16.6′N, 94°33.4′W, *Valdivia 744* (XAL); Hidalgotitlán, 150 m, *Valdivia 1351* (XAL); near La Escuadra, 160 m, 17°19′N, 94°38.5′W, *Valdivia 1330* (XAL); Mpio. J. de Ferrer, Cerro de Villa Rica, near Plan de la Flor, 1250 m, 19°48′N, 96°46′W, *Castillo et al. 1715* (F); Mpio. Jesús Carranza, 2 km N del Poblado 2, Ejido F. J. Mina, 120 m, 17°16′N, 94°40′W, *Vásquez & Navarrete 2383* (MO); Mpio. Pajapan, Volcán San Martín Pajapan, 6 km NW of Pajapan, 1200 m, 18°18′20″N, 94°43′30″W, *Nee et al. 24974* (F, MO); Sontecomapan–Montepío, N of San Andrés Tuxtla, 150–200 m, 18°42′N, 95°10′W, *Croat & Hannon 63158* (MO, NY, US); Mpio. Tlapacoyan, Río Tablazos, Tlapacoyan–Altotonga, 6 km SSW of Tlapacoyan, 19°56′N, 97°13′W, *Nee et al. 26090*

(F, MO, NY); Vallé de Córdova, *Bourgeau 2296* (K, P). NICARAGUA. **Estelí**: El Zacatón (Plan Helado), ca. 1300 m, 13°13′N, 86°14′W, *Moreno 17521* (MO); Laguna de Miraflores, ca. 1200 m, *Grijalva 952* (MO). **Jinotega**: ca. 5–8 mi. SW of Jinotega, 1500 m, *Croat 43084* (CM, MO); San Ramón–Paricutín, Comarca Kilambé, SE of Cerro Kilambé, 800–900 m, 13°35′N, 85°40′W, *Moreno 7687* (MO); along Hwy. 3 ca. 1 km NW of La Fundadora entrance, 1450–1520 m, 13°01′N, 85°56′W, *Stevens & Henrich 20435* (MO), Las Camelias–La Salvadora, 1100–1150 m, 13°05–06′N, 85°53–54′W, *Stevens et al. 15327* (MO); N slope of Volcán Yalí, 1200–1400 m, 13°15′N, 86°10′W, *Stevens et al. 15091* (MO); Matagalpa–Jinotega Road, Km 146, 1200–1400 m, *Moreno 571* (MO); Laguna Miraflores, ca. 26.1 km NE of Hwy. 1 at Estelí, 1250–1300 m, ca. 13°15′N, 86°15′W, *Henrich & Stevens 243* (MO); Las Camelias–La Salvadora, road from Hwy. 3 through La Fundadora, 1100–1150 m, ca. 13°05–06′N, 85°53–54′W, *Stevens & Grijalva 15322* (MO); Macizos de Peñas Blancas, vic. of Finca of Manuel Estrada (El Cielo), 1200–1400 m, ca. 13°15′N, 85°41′W, *Stevens 11665* (MO); 1500–1650 m, ca. 13°15–16′N, 85°41′W, *Stevens 11430* (MO); Río Bocay, Salto Kayaska, 190–340 m, ca. 13°51′N, 85°22′W, *Stevens et al. 16479* (MO). **Matagalpa**: Valle de Arenal, on road to Sanatorio de Aranjuez, 1400 m, 13°02′N, 85°55′W, *Davidse et al. 30444* (MO); 13°01′N, 85°54′W, *Moreno 9583* (MO); Fuente Pura, km 142, 1400–1450 m, 13°N, 85°55′W, *Moreno 17017* (MO); road to Cerro La Carlota, 2 km from Tuma, 1040–1100 m, 12°58′N, 85°52′W, *Moreno 15659* (MO); Cerro Picacho, behind La Selva Negra Hotel, 1200–1540 m, 13°N, 85°55′W, *Davidse et al. 30311* (MO). **Nueva Segovia**: Río San Fernando Valley, Cerro El Peñascal, 800–1125 m, 13°2–3′N, 86°19–20′W, *Stevens 3297* (BM, MO). **Río San Juan**: Bocas de Sábalo, 70–100 m, 11°03′N, 84°27′W, *Moreno 26692* (MO). **Zelaya**: El Empalme–Limbaika, junction of road to Alamikamba, ca. 25 m, ca. 13°32′N, 84°30′W, *Stevens 12739* (MO); road to Mina Nueva América, ca. 10 km N of main road, *Stevens 12673* (MO); ca. 11.3 km N of main road, *Pipoly 5283* (MO); ca. 6.3 km S of bridge at Colonia Yolania, ca. 200–300 m, ca. 11°36–37′N, 84°22′W, *Stevens 4824* (MO); Cerro El Hormiguero, W range, ca. 1100–1183 m, ca. 13°44′N, 85°W, *Pipoly 5198* (MO); *5194* (MO); *5190* (MO); Cerro La Pimienta number 1, ca. 900–980 m, ca. 13°45′N, 84°59′W, *5107* (MO); *5114* (MO); ca. 13 km above Kururia, on road to San Jerónimo, <200 m, *Pipoly 3826* (MO); 1 km S of Monkey Point, ca. 5 m, 11°35′N, 83°39′W, *Moreno & Sandino 12531* (MO); Monkey Point, 1.5 km NW, 1–5 m, 11°36′N, 83°38′W, *Moreno & Sandino 11957* (MO); Río Kisalaya, near Tala Has and Puente Mango, 40–60 m, ca. 14°41′N, 84°03′W, *Stevens 7628* (BM, MO); Río Mico, near El Recreo, ca. 30 m, *Standley 19404* (F); *19525* (EAP, F), *19614* (F); Río Pis Pis, 0.5–1.5 km from Plantel El Salto, road to Bonanza, ca. 140 m, ca. 14°03′N, 84°37′W, *Stevens 18871* (MO); Río Punta Gorda, Atlanta, ca. 10 m, 11°34′N, 84°01′W, *Moreno & Sandino 12770* (MO); Waspam–Puerto Cabezas, Río Troncera, <200 m, ca. 14°43′N, 84°06′W, *Pipoly 4055* (MO). PANAMA. **Bocas del Toro**: Gualaca–Chiriquí Grande, 4.2 mi. E of Chiriquí Grande, ca. 0 m, 8°55′N, 82°09′W, *Croat 66814* (MO); 0.4 mi. SE of Punta Peña, 120 m, 8°57′N, 8°56′W, *Croat 74939* (AAU, CR, MO, NY); Fortuna Dam area, N of Fortuna Dam, 650–700 m, 8°45′N, 82°15′W, *McPherson 11131* (MO); Chiriquí Grande–Fortuna, 1.6 mi. N of Continental Divide, 770–790 m, 8°45′N, 82°17′W, *Croat & Zhu 76453A* (MO), *76456A* (CM, MO); 10 mi. N Divide, 1 mi. N from highway, 130 m, 8°46′N, 82°11′W, *Hammel et al. 14598* (MO); 4.3 km N of Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60210* (CM, MO); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60259* (CAS, CR, F, KYO, M, MEXU, MO, PMA). **Canal Area**: Frijoles–Monte Lirio, 30 m, *Killip 12133* (US); hills N of Frijoles, *Standley 27598* (US); Pipeline Road, 14 mi. NW of Gamboa gate, *Croat 12363* (MO); Barro Colorado Island, *Croat 6472* (F, MO, RSA, SCZ); *Aviles 25* (F); *46* (F); Gatún Lake, *Standley 31398* (US); *Croat 6531* (F, MO, SCZ), *6334* (MO), *5052* (MO), *10901* (MO), *8290* (MO), *10859* (MO), *9018* (MO), *8999* (MO), *10076* (MO); *Silvestre s.n.* (MO); *Croat 6023* (MO); Summit Gardens, *Croat 59139* (MO), *17155* (MO), *10768* (MO), *17060A* (MO). **Chiriquí**: Finca Ojo de Agua, 1300 m, 8°51′N, 82°46′W, *Knapp 1590* (MO); Cañas Gordas–Volcán, 1 m E of Cañas Gordas, ca. 1000 m, *Croat 22304* (MO); 8 mi. W of Puerto Armuelles, in vic. of San Bartolo Límite, ca. 600 m, *Croat 22022* (MO), *22026* (MO); Cerro Colorado, above San Félix, 15–18 mi. N of Pan-American Highway, 800–1000 m, *Croat 33179* (CM, MO); Gualaca–Chiriquí Grande, Fortuna Dam area, 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *Croat 67843* (CM, MO); 5.9 mi. NW of Los Planes de Hornito, 1225 m, 8°45′N, 82°14′W, *Croat 67795* (CR, MO, PMA); 1400 m, *Croat 48719* (MO); *48697* (MO); *48681* (MO); Gualaca–Chiriquí Grande, 8 mi. beyond Los Planes de Hornito, trail to Río Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67918* (CAS, COL, L, MEXU, MO, PMA, US); 10.1 mi. NW of Los Planes de Hornito, 1250 m, 82°17′W, 8°45′N, *Croat 50040* (CM, MO); Quebrada Los Chorros–Quebrada Honda, N of Fortuna Lake, 1100 m, 8°45′N, 82°14′W, *Churchill & Churchill 6107* (MO); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60056* (B, CAS, F, L, MBM, MO, P, PMA); Cerro Colorado, 2.3 km above Chame, 1000 m, *Croat 37067* (MO). **Coclé**: Penonomé–Coclecito, Río Cascajal, 5.7 mi. N of Llano Grande, 210 m, 8°40′N, 80°26′W, *Croat 67541* (CR, MO); El Copé region, 9.4 km above El Copé, 750–900 m, *Croat 44726* (MO); Alto Calvario, 710–800 m, *Croat 68716* (EAP, G, HNMN, MO, TEX); 8°39′N, 80°36′W, *68849* (MO); 580–740 m, 8°38′N, 80°36′W, *Croat 67522* (MO, US); El Valle region, La Mesa, above El Valle de Antón, 860–900 m, *Croat 37407* (MO); 870 m, 8°50′N, 80°07′W, *Hoover 1320* (MO); 800–900 m, 8°38′N, 80°09′W, *Croat 67152* (B, CAS, CM, COL, DUKE, F, K, L, MEXU, MO, NY, PMA, QCA, TEX, VDB, WIS); 800 m, 8°36′N, 80°07′W, *Croat & Zhu 76691* (MO); Cerro Gaital, *Churchill 3907* (MO). **Colón**: Sabanitas–Portobelo, Río Piedras Lumber Road, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75159* (MO); Río Indio–Miguel de la Borda, 0 m, *Croat 36906* (MO); Miguel de la Borda, *Croat 9856* (F, MO, RSA, US); Santa Rita Ridge Road, 10.6 km from highway, ca. 380 m, *Croat 34345* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76964* (MO); along Río Guanche ca. 2 km E of bridge on the main Puerto Pilón–Portobelo Road, 100 m, 9°30′N, 79°39′W, *Croat 75176* (MO). **Darién**: Cerro Pirre region, middle slopes on W side, 550–760 m, 7°57′N, 77°46″W, *Croat 68958* (MO); *68893* (MO); Río Cana–Río Escucha Ruido, above Cana Gold Mine, 1310–1430 m, *Croat 37755* (MO); *37818* (MO); *37827* (MO); S of El Real, Alturas de Nique, near Cana mine, along old Camino Real toward Colombia, 800–1000 m, 7°45′N, 77°40′W, *McPherson 11536* (MO); Río Cocalito, ca. 5 mi. from P. Cocalito, *Whitefoord & Eddy 222* (BM, MO); Parque Nacional del Darién, Panama–Colombia border, Río Pucuro, Cerro Tacarcuna, ca. 6

km N of Cerro Mali, 1300–1500 m, 8°09.5′N, 77°15′W, *Hammel et al. 16537* (MO, PMA). **Herrera**: Las Minas, Primer Ciclo de Chepo, 900 m, 7°43′N, 80°50′W, *Galdames et al. 1765* (MO); 18 km W of Las Minas, Alto Higo, N slope, 2400 ft., *Hammel 4227* (MO). **Los Santos**: Azuero Peninsula, Jobero–Río Pedregal, 300–700 m, *Croat 34479* (MO); Río Guanico valley, 600 m, 7°18′N, 80°30′W, *McPherson 9245* (MO, NY, SCZ). **Panamá**: Cerro Azul, *Croat 17281* (MO); El Llano–Cartí Road, ca. 16–18 km N of Pan-American Highway, 400 m, *Tyson & Nee 7352* (MO); Mile 5–9, 200–250 m, 9°15–16′N, 78°59′N, *Thompson 4624* (CM); Mile 10, 330 m, *Croat 33823* (CM, F, MO, TEX, WIS); Mile 7, 460 m, *75109* (MO); Km 7–12, 360–400 m, *25096* (MO); Mile 8.2, 450 m, 9°14′N, 79°W, *Knapp & Huft 4412* (MO); Mile 12, 200–500 m, *Liesner 695* (MO); Mile 5–9, 200–250 m, 9°15–16′N, 78°59′W, *Thompson 4636* (CM); Cerro Campana, 800 m, 8°41′N, 79°56′W, *Croat 74770* (AAU, MO); *74771* (MO, PMA); *17177* (MO); ca. 850 m, 8°40′N, 79°50′W, *Thompson 4577* (CM); 700 m, 79°55′W, 8°40′N, *Hamilton et al. 1174* (MO); *Hammel 5561* (MO); ca. 1 mi. from Inter-American Highway, ca. 150 m, *Croat 35983* (MO); *12063* (MO); 800 m, 8°41′N, 79°56′W, *74770* (MO); Cerro Jefe region, near summit 750–800 m, 9°14′N, 79°22′W, *Croat 67087* (F, MO); 800–1000 m, *Gentry 2892* (GH, MO); 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76608* (CR, GB, MBM, MEXU, MO, NY); 4.6 km beyond peak, on road to Altos de Pacora, 26.3 km from highway, ca. 600 m, *Croat 35933* (MO); 3–3.5 mi. NE of Altos de Pacora, 11.1–11.6 mi. beyond Lago Cerro Azul, 700–750 m, 9°15′N, 79°25′W, *Croat 68695* (MO, PMA). **San Blas**: beach E of Puerto Obaldía, *Croat 16910* (MO); *16911* (MO); *16914* (MO); 7 mi. N of Inter-American Highway, 550 m, 9°43′N, 78°68′W, *Croat 60506* (MO); Cerro Brewster, 800–850 m, 9°18′N, 79°16′W, *de Nevers et al. 6287* (MO); El Llano–Cartí Road, vic. Nusagandi, 450 m, 9°18′N, 79°59′W, *Croat 75150* (CM, MO, PMA); 350 m, 9°20′N, 79°W, *Croat & Zhu 77012* (CM, MO). **Veraguas**: Dist. Montijo, Isla de Coiba, 7°37′N, 81°44′W, *Galdames et al. 2213* (PMA); *2073* (CM, MO, PMA); 400 ft., *Antonio 2383* (MO); *2343* (MO, PMA); 400 m, 7°31′N, 81°51′W, *Galdames et al. 2284* (MO, PMA); 50 m, 7°35′N, 81°47′W, *Galdames 2256* (MO, PMA); Santa Fe region, 7 km W of Santa Fe, 2900 ft., *Nee 11192* (MO, RSA); Cerro Tute, to 1200 m, *Witherspoon et al. 8873* (MO); Santa Fe–Río San Luis, at Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66886* (MO, PMA); *66916* (MO, PMA), *66920* (MO).

Philodendron scalarinerve Croat & Grayum, sp. nov. TYPE: Panama. Panamá: road past and 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan-American Hwy., 11.1–11.6 mi. beyond Lago Cerro Azul, 700–750 m, 9°15′N, 79°25′W, *Croat 68692* (holotype, MO–3585744; isotypes, B, CAS, COL, CR, F, K, NY, PMA, US). Figures 357–363.

Planta hemiepiphytica; internodia 1–1.5(3) cm longa, 1.5–3.5(4) cm diam.; cataphylla usque 22 cm longa, incostata vel obtuse 1-costata, raro acute 2-costata, persistentia semi-intacta; petiolus subteres, 20–75 cm longus, 0.7–1.5 cm diam.; lamina oblong-elliptica vel leniter cordata, 33–67 cm longa, 11.4–40 cm lata, cum nervis conspicue scalariformibus inter nervos minores; inflorescentia 1–4; pedunculus 6–20 cm longus, subteres; spatha 16–21.5 cm longa, pallide viridis; lamina spathae seminitida, extus striata alba apice, intus viridi diluta; tubo spathae hebetato, extus striato albo basi, intus viridalbo; pistilla 4–6(7–8)-locularia; loculi (10)12–14-ovulati.

Appressed-climbing hemiepiphyte; stems moderately short; leaf scars conspicuous, 2–4 cm wide; internodes 1–1.5(3) cm long, 1.5–3.5(4) cm diam., about as long as broad; roots moderately few per node, short, drying dark brown, matte, longitudinally ridged; cataphylls moderately thick, to 22 cm long, unribbed to bluntly 1-ribbed, rarely sharply 2-ribbed, drying dark brown, persisting semi-intact, eventually fibrous at upper nodes. LEAVES erect-spreading, clustered at or near stem apex; **petioles** 20–75 cm long, 0.7–1.5 cm diam., subterete, stiff, green, obtusely flattened, sulcate adaxially; sheathing 1–2.5 cm long; geniculum scarcely thicker than petiole, 6–7.8 cm long slightly paler than petiole; **blades** oblong-elliptic to narrowly ovate, moderately coriaceous, acuminate at apex (the acumen sometimes inrolled, to 2 mm long), obtuse to subcordate at base, 33–67 cm long, 11.4–40 cm wide (1.2–4 times longer than wide), (0.82–2.11 times longer than petiole), broadest at the middle, margins weakly undulate, upper surface dark green, semiglossy, lower surface much paler, matte to semiglossy, obscurely dark-punctate at 10× magnification; midrib convex to narrowly raised, sometimes paler than surface above, convex to thicker than broad and concolorous below; basal veins 1–4 per side, with all free to base; primary lateral veins 5–18 per side, departing midrib at a 60–75° angle, arcuate-ascending to the margins, sunken above; minor veins arising from the midrib only; with scalariform "cross-veins" weakly visible when fresh, conspicuously raised above on drying, barely visible below. INFLORESCENCES spreading, pendent, shorter than leaves, 1–4 per axil; peduncle 6–20 cm long, subterete, white-streaked near apex, spongy; **spathe** 16–21.5 cm long (0.6–1.4 times longer than peduncle), pale green, acuminate at apex, obtuse at base, convolute to about the middle at anthesis; spathe blade semiglossy, white-streaked at apex outside, light green inside; spathe tube matte, white-streaked at base outside, 5–7 cm long, 2–3.5 cm diam., greenish white inside; **spadix** sessile, erect, (7.6)9–12 cm long, broadest at the base or at the middle or below the middle; pistillate portion light green, slightly tapered above middle or toward both ends, (1.7)2.6–4.3(7.8) cm long, 0.8–1.3 cm diam. at apex, 0.8–1.4 cm diam. at middle, 0.9–1.4 cm wide at base; staminate portion 4.8–8.7 cm long; fertile staminate portion (9)12 mm diam. at base, (9)12 mm diam. at middle, (6)10 mm diam.

ca. 1 cm from apex, broadest at the base, slightly narrower than the pistillate portion, slightly narrower than the sterile portion; sterile staminate portion as broad as the pistillate portion, 1.2–1.4 cm diam.; pistils (1.4)2.3–2.8(3.2) mm long, (1)1.4–1.9 mm diam.; ovary 4–6(7–8)-locular, (0.7)1.5–1.8(3) mm long, (1.1)1.5–1.9 mm diam., with axile placentation; locules (0.7)1.5–1.8(3) mm long, 0.4–0.6 mm diam.; ovules (10)12–14 per locule, 2-seriate, (0.1)0.3–0.4 mm long, longer than funicle; funicle 0.1–0.2(0.3) mm long, adnate to lower part of partition, style 0.5(0.7) mm long, 1.1–1.4(2.2) mm diam., similar to style type B; style apex usually flat, sometimes rounded or domed, with stigma lobes over depressions (if apex is flat or domed); stigma usually lobed, sometimes subdiscoid or truncate, lobed, 0.9–1.2(1.4–1.7) mm diam., (0.1)0.2–0.3 mm high, covering entire style apex, inserted on center of style apex, sometimes medially depressed; the androecium truncate, prismatic, sometimes weakly oblong to oblong, margins 4–6-sided, sometimes scalloped, (0.6)0.8–1.1 mm long, 1–1.8 mm diam. at apex; thecae oblong, 0.3–0.5 mm wide, ± parallel to one another, contiguous or nearly contiguous; pollen ellipsoidal, <0.1 mm long, <0.1 mm diam.; sterile staminate flowers irregularly 4–6-sided, clavate or weakly rounded, blunt, rarely irregularly 3–5-sided or depressed with a furrow, (0.8–1.2)1.7 mm long, 0.9–1.5(1.5–2 mm) wide.

Flowering in *Philodendron scalarinerve* occurs principally in the early rainy season (June through August) but also in March. Post-anthesis inflorescences have been collected primarily from June through September, but one such Costa Rican collection was made in January and one South American collection in December. Immature fruiting collections are known from July through December.

Philodendron scalarinerve ranges from Costa Rica to Ecuador, from sea level to 1325 m in *Tropical wet forest, Premontane rain forest, Tropical Lower Montane rain forest,* and *Tropical rain forest* (Colombia).

Philodendron scalarinerve is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its short internodes, bluntly 1-ribbed to unribbed cataphylls persisting as pale fibers with small fragments of thin, pale epidermis, terete to subterete petioles, narrowly ovate to oblong-ovate blades drying dark with the "cross-veins" (tertiary veins that extend between the minor veins) numerous and conspicuous on both surfaces and uniformly greenish spathes.

Additional specimens examined. COSTA RICA. **Heredia**: Finca El Bejuco, N of Río Sarapiquí, Chilamate de Sarapiquí, ca. 100 m, 10°27′N, 84°04′W, *Grayum & Ray 5564* (CR, MO); Cerros Sardinal, ca. 2–2.5 km N of Chilamate de Sarapiquí, 80–160 m, 10°28′N, 84°04′W, *Grayum et al. 6147* (CR, MO). **Limón**: Cerro Coronel, S of Río Colorado, 10–80 m, 10°40′30″N, 83°39′30″W, *Davidse & Herrera 31475* (CR, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 4.3 km N of the Continental Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60173* (CM, MO); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60251* (MO, NY, PMA, QCA). **Chiriquí**: Fortuna Lake area, Río Chiriquí Valley, vic. IRHE facilities, 1100–1200 m, 8°45′N, 82°18′W, *Croat 66593* (AAU, CAS, CM, COL, DUKE, G, GH, HUA, K, L, MEXU, MO, NY, PMA, QCA, TEX, US, VDB, VEN); Lago Fortuna, along trail to Río Hornito, 8°45′N, 82°18′W, *Croat & Zhu 76419* (MEXU, MO, SCZ, US). **Coclé**: El Copé region, 5–6 mi. N of El Copé, 600–800 m, 8°38′N, 8°35′W, *Croat & Zhu 77222* (HUA, MO, MY, QCNE); ca. 0.5 mi. N of Continental Divide at Alto Calvario, ca. 5.5 mi. N of El Copé, 800 m, 8°39′N, 80°36′W, *Croat 75081* (MO, US); Alto Calvario, ca. 6 km N of El Copé, 710–800 m, 8°39′N, 80°36′W, *Croat 68723* (MO, PMA, RSA); 720–800 m, 8°38′N, 80°35′W, *McPherson 12856* (BR, CAS, CR, MO, PMA); 930 m, *Croat 49196* (CAS, L, MO); *49174* (MO), *49154* (MO); *68722* (DUKE, F, MO, PMA); 750–900 m, *44737* (CM, MO); *44720* (MO, PMA); El Valle region, La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, *Croat 67203* (CR, MO, PMA, QCA, US); *25436* (F, MO); 880 m, *37569* (F, MO); ca. 1000 m, *Kennedy & Dressler 1759* (MO); *Luteyn & Kennedy 1717* (DUKE); Cerro Gaital, 800–900 m, 8°37′N, 80°07′W, *McPherson 11196* (MO, PMA). **Colón**: Santa Rita Ridge Road, ca. 22 km from Highway, 500 m, 9°25′N, 79°40′W, *Hammel et al. 14478* (MO). **Panamá**: Vertiente Pacifica, 150–200 m, 9°13.5′N, 78°15′W, *Herrera 1604* (K, MO, PMA, STRI, US); Cerro Jefe region, 26.3 km from highway, ca. 600 m, *Croat 35919* (MO); Campo Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Croat 22701A* (CM, MO, NY); 700 m, *Croat 27072* (F, MO), *27093* (MO); ca. 1 mi. beyond Alto de Pacora, 2600 ft., *Hammel & Kress 13420* (DUKE); El Llano–Cartí, 5–6 mi. N of Inter-American Highway at El Llano, 350–375 m, *Croat 34805A* (F, MO, NY, QCA, WIS); Mile 6.8, 350 m, *Croat 49112* (MO); Mile 7, 9°19′N, 79°59′W, *Croat 75103* (CM, MO). **San Blas**: Nusagandi, 300 m, 9°15′N, 79°W, *McPherson 11066* (MO, PMA); Río Urgandi–Cerro Óbu, on trail, 100–300 m, 9°23′N, 78°48′W, *de Nevers et al. 8019* (MO, PMA); Río Diablo, 40 m, 9°23′N, 78°34′W, *Herrera et al. 1714* (MEXU, MO, PMA, STRI, US). **Veraguas**: Santa Fe region, slopes of Cerro Tute, NW of Santa Fe, 1250–1350 m, *Croat 48971* (F, MO, W); Santa Fe–Río San Luis, 8 mi. N of school, 450 m, 8°33′N, 81°08′W, *Croat 66959* (CM, ENCB, MBM, MO, PMA, QCA); Alto Piedra–Calovébora, Río Dos Bocas Valley, 350–400 m, *Croat 27367* (F, MO, PMA, US).

COLOMBIA. **Chocó**: Medellín–Quibdó, 78 km W of Bolívar, 466 m, *Croat 49286* (MO); Km 175–176, 117–118 km E of Quibdó, 465 m, 5°44′N, 76°28′W, *Croat 57485* (CHOCO, COL, JAUM, K, MO, US); Quibdó–Istmina, Km 14, <100 m, 5°32′N, 67°37′W, *Croat & Cogollo 52215* (MO); S of Río Rancherita, Km 31–32, <50 m, 5°27′N, 76°39′W, *Croat 57372* (CHOCO, COL, JAUM, MO); Quibdó–Lloro, vic. Río Atrato, ca. 150 m, 5°29′N, 76°35′W, *Croat 55979* (COL, JAUM, MO, NY); Río Capá–Río Mumbú, upriver from Lloro, 80–120 m, 5°37′N, 76°25′W, *Juncosa 1457* (MO); Quibdó–Yuto, 12 km S of

Quibdó, 60 m, 5°38′N, 76°40′W, *Croat 56261A* (CM, MO); Serranía de Baudó, Las Animas–Pato (Río Pato), 4 km S of Pato, 150 m, 5°30′N, 76°46′W, *Croat 56151* (MO); Jequedó, 41 km W of Las Animas, ca. 10 km E of Río Pato, 220 m, *Gentry & Rentería 24112* (MO). **Nariño**: Mpio. Barbacoas, Reserva Natural Río Ñambí, 1325 m, 1°18′N, 78°08′W, *Betancur et al. 4778* (MO). **Valle**: Bajo Calima region, Buenaventura–Río Calima, 6.5 km beyond Portón Tomar, 50 m, 4°02′N, 77°07′W, *Croat 61278* (AAU, B, CAS, CM, COL, CR, F, K, L, MO, NY, QCA, US); *61380* (CM, MO); road to Málaga, 6 km S of main road, 50–80 m, 3°56′N, 77°07′30″W, *Croat 69417* (AAU, COL, CR, GB, MEXU, MO, NY, QCA); 100 m, 3°55′N, 77°W, *Monsalve 892* (MO); Buenaventura–Málaga, Km 65–66, 40–65 m, 4°10′N, 77°12′W, *Croat 71055* (MO); at Km 17.5, 3°57′N, 77°01′W, *Croat & Bay 75630* (MO); Km 28, W of Buenaventura–Málaga road, 3°59′N, 77°03′W, *Bay 269* (MO); Km 35.2, 100 m, 4°N, 77°03′W, *Croat & Bay 75759* (MO); Km 44, <100 m, 4°03′N, 77°08′W, *Croat & Watt 70199* (COL, MO, NY, US); Km 52.4, 140 m, 4°03′N, 77°05′W, *Croat & Bay 75724* (MO); *75728* (MO); 11 km NW of Cali–Buenaventura Highway, 3°56′30″N, 77°01′W, *Croat 69321* (CM, MO). ECUADOR. **Carchi**: Chical, 1200–1250 m, 0°56′N, 78°11′W, *Thompson & Rawlins 761* (CM, MO).

Philodendron schottianum H. Wendl. ex Schott, Oesterr. Bot. Z. 15: 72. 1865. TYPE: Costa Rica. *Wendland s.n.* (holotype, W? lost). Schott ic. 2735–36 (neotype, here designated, W). Figures 2, 17, 365–371.

Usually epiphytic or hemiepiphytic; stem appressed-climbing, grayish green, sap strongly thyme-scented; internodes short, thick, semiglossy, 4–7.5 cm diam., broader than long, pale green to gray, epidermis thin, yellow, fragmented, without fissures; roots moderately few per node, drying dark brown to ca. 5 mm diam., epidermis semiglossy, flaking; cataphylls 16–46 cm long, sharply 2-ribbed (ribs to 1.5 cm high), usually tinged red, drying brownish yellow, often glossy (as if surface is shellacked), broadly concave to broadly D-shaped adaxially, persisting semi-intact, finally as a dense mass of whitish fibers; margins acute; **petioles** 35–83 cm long, 1–2.2 cm diam., subterete to D-shaped, firm to moderately spongy, medium green, drying yellowish brown, obtusely flattened with obtuse medial rib toward apex adaxially, surface semiglossy and obtusely striate; **blades** ovate, subcoriaceous, semiglossy, moderately bicolorous, acuminate to abruptly acuminate at apex (the acumen strongly inrolled, 2–8 mm long), cordate to sagittate at base, 30–77 cm long, (17.5)23–64 cm wide (1–1.7(2.7) times longer than wide), (0.6–1.2 times longer than petiole); upper surface dark green, semiglossy to subvelvety-matte; lower surface semiglossy or rarely matte, moderately paler; anterior lobe 23–57 cm long, 24.5–64 cm wide (1.6–2.7 times longer than posterior lobes); posterior lobes 8.5–28 cm long, 10–29.6 cm wide, obtuse to broadly obtuse; sinus usually spathulate, 8–20 cm deep; midrib flat to broadly convex, paler than surface above, convex to narrowly rounded, concolorous or slightly darker than surface below; basal veins (1)6–7(8–9) per side, with 0–1(2) free to base, most of the remainder coalesced 1–5.5 cm, 2 coalesced to 11 cm; posterior rib usually naked, 1–3 cm long; primary lateral veins 3–8 per side, departing midrib at a usually 40–70° angle, quilted-sunken to sunken, paler than surface above, convex and slightly paler than surface below; tertiary veins visible and darker than surface below; minor veins conspicuous, arising from both the midrib and primary lateral veins, moderately prominulous on drying, alternating with secretory ducts perpendicular or more frequently oblique, sometimes branching; "cross-veins" weakly parted. INFLORESCENCES erect to erect-spreading, (1)2–3 per axil; peduncle 2–9 cm long, 8–14 cm diam., pinkish red, white striate, especially toward apex; **spathe** 10–17 cm long (1.9–7 times longer than peduncle), weakly constricted, oblong-ellipsoid; spathe blade light green outside, cream, pale lineate in upper one-half inside; spathe tube green, tinged red outside, 6–9 cm long, red with conspicuous resin canals inside; **spadix** tapered to somewhat ovate, weakly protruding, 8.8–14.4 cm long; pistillate portion weakly ovoid, whitish, (2)3–4.9 cm long, 2–2.4 cm diam. throughout, 1.4–1.5 cm diam. at apex, 1.4–1.9 cm diam. at middle, 1.4–1.8 cm wide at base; staminate portion 5.7–10.8 cm long; fertile staminate portion bluntly tapered at apex, 1.1–1.4 cm diam. at base, 1.2–2.3 cm diam. at middle, 1(1.7) cm diam. ca. 1 cm from apex, broadest at upper two-thirds, broader than the pistillate portion, slightly narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, 1.4–2.5 cm diam.; pistils (1)3–3.9 mm long, 1.5–1.9(3.8) mm diam., margins broadly rounded and slightly raised above the apex; ovary 4–6-locular, 1.9–2.5 mm long, 1.3–1.9(3.8) mm diam., with axile placentation; locules 1.9–2.5 mm long, 0.4–0.7 mm diam.; ovule sac not present or to 1.9 mm long; ovules 10–14(18) per locule, 2-seriate, rarely contained within translucent or transparent envelope, 0.1–0.3 mm long, longer than funicle; funicle 0.1–0.3 mm long, adnate to lower part of partition, style 0.8–1.2 mm long, 1.5–1.9(3.6) mm diam., similar to style type B; style apex barely raised, button-like, broadly concave, medial apex with a whitened margin, raised and apparently like type D on drying; stigma subdiscoid, truncate, 1.4–1.6 mm diam., 0.3–0.4 mm high, covering ± entire style apex, sometimes de-

pressed shallowly and medially; the androecium truncate, oblong, prismatic, margins irregularly 4–5-sided, sometimes scalloped, 1 mm long, 1.8–2.1 mm diam. at apex; thecae ± oblong, 0.4–0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregularly 4–6-sided, prismatic, 2.5–3.5 mm long, (1.4)1.8–2.2 mm wide. INFRUCTESCENCE with pistillate spadix 5–6 cm long, 3.5 cm diam.; berries white, 1.1 cm long, 4–4.6 mm diam.; seeds 1.4 mm long, 0.5 mm diam., cream-colored.

Flowering specimens of *Philodendron schottianum* have been collected only from March and June, but post-anthesis collections have been made from March through August. Immature fruiting collections have been collected from January, May, September, and November. The immature January fruiting collection is a clear indication that the species must flower much earlier in the dry season than March (as indicated above). Perhaps it flowers throughout the dry season. In the cloud forest regions where this species occurs the dry season would not be very severe.

Philodendron schottianum ranges from Costa Rica to Panama at (490)730 to 2250 m in *Premontane rain forest* and *Tropical Lower Montane wet forest* life zones. In Panama, this species ranges no further east than Veraguas (Cerro Tute), except for a disjunct occurrence on Cerro Jefe in Panamá Province. All Costa Rican collections are from the northern slopes of the Cordillera Central in Alajuela, Heredia, and San José, and the northern end of the Cordillera de Talamanca in the Tapantí region of Cartago Province. It is to be expected throughout much of the Cordillera de Talamanca.

Philodendron schottianum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its short, thick internodes; sharply 2-ribbed cataphylls persisting as a dense mass of fibers (frequently with patches of glossy, yellowish to orange-brown epidermis); obtusely to sharply D-shaped petioles drying somewhat grayish or rarely yellowish and glossy; large, broadly ovate blades with a deep, usually spathulate sinus, usually pale-drying primary lateral veins; and rather conspicuous secretory canals between the veins; 2–3 short-pedunculate inflorescences per axil; and scarcely constricted, externally green spathes red on the tube within.

In Costa Rica and at higher elevations in Panama, such as on Cerro Colorado and on Cerro Pate de Macho (1000 to 2200 m), the petioles are subterete or obtusely flattened adaxially. At lower elevations in Bocas del Toro, Veraguas, and Coclé, the petioles become D-shaped to sharply D-shaped with erect margins, and at the lowest elevations they are nearly always wing-margined.

In Bocas del Toro Province, Panama, at middle elevations and in mesic situations, this species is most easily confused with *P. findens,* which also has sharply D-shaped petioles. *Philodendron findens* also has spathes which, like those of *P. schottianum,* are barely constricted midway. In rare situations where the blades of *P. findens* do not promptly tear into narrow segments, *P. findens* can be distinguished from *P. schottianum* by having primary lateral veins of the lower surface drying darker than the surface.

In central Panama, *P. schottianum* can also be confused with *P. llanense.* Both *P. schottianum* and *P. llanense* occur in the Cerro Jefe region, though *P. schottianum* has been collected there only once, northeast of Altos de Pacora. This collection (*Croat 68691*) exhibits most of the diagnostic features of *P. schottianum,* especially the persistent yellowish, semi-intact cataphylls, and the acutely D-shaped petioles with an obtuse medial rib (unknown in *P. llanense*), but has a blade shape midway between that of *P. schottianum* and *P. llanense* (blade length/width ratio 1.5 vs. an average of 1.4 for *P. llanense* and 1.65 for *P. schottianum*). *Philodendron llanense* differs in having at most obtusely flattened petioles and in lacking the conspicuous yellowish cataphylls of *P. schottianum. Philodendron llanense* also rarely occurs above 500 m (to 950 m), whereas *P. schottianum* only rarely occurs to as low as 500 m.

Philodendron schottianum can be confused with *P. thalassicum* and *P. alticola,* especially in Costa Rica. *Philodendron thalassicum* differs in having bluish green leaf blades that are glaucous beneath and sharply D-shaped petioles drying somewhat blackened rather than merely obtusely flattened and light yellow-brown, as in *P. schottianum. Philodendron alticola* differs in usually having narrower leaf blades (usually more than 1.8 times longer than wide) and stigma tubes exserted as minute funnels on the dried stigma.

Philodendron dodsonii may also be confused with *P. schottianum.* The former differs in occurring usually at lower elevations principally in tropical wet forest and premontane wet forest, and in having larger leaf blades, more long-pedunculate inflorescences, and longer spathes with a normal constriction above the spathe tube.

One collection, *Grayum 7333,* differs from more typical collections in having blades reportedly matte on both surfaces and lacking prominulous minor veins and conspicuous secretory ducts (so evident in other material of this species where they

alternate with the minor veins). In addition, this specimen has darker-drying petioles and more fragmentary old cataphylls as well as intact cataphylls (perhaps juvenile?) drying brown (rather than the typical brownish yellow) and a spathe with a narrowly acuminate portion extending a full 5 cm beyond the end of the spadix. On other specimens, the spadix ends only about 1 cm or less short of the end of the spathe.

Hammel et al. 14705 is unusual in lacking cataphylls, suggesting that they might have been deciduous (or forcibly removed during preparation).

Additional specimens examined. COSTA RICA. **Alajuela**: 3.5–4 mi. W of center of San Ramón, ca. 800 m, *Croat 46813* (MO); Atlantic side of Alto Palomo, 1900 m, *Lent 1845* (CR, F); Río Gorrión–Río Toro, 1700 m, 10°12′N, 84°19′W, *2996* (CR, F); Río Cariblanco Canyon, Río Cariblanco–Quebrada Quicuyal, SW of Cariblanco, 840–950 m, 10°16′N, 84°12′W, *Grayum et al. 6186* (CR, MO, NY); Río Sarapiquí, road to Colonia Virgen del Socorro, 830 m, 10°16′N, 84°11′W, *Croat 68341* (CR, MO). **Cartago**: 31 km from San José, SE of CR-2, 1750 m, *Harmon & Fuentes 6081* (UMO); Tapantí Watershed Preserve, ca. 20 mi. SW of Paraíso, 1500–1800 m, 9°43′N, 83°47′W, *Croat 47047* (MO); 1500–1800 m, *Croat & Grayum 68293* (B, K, MO); 1500–1700 m, Croat *36110* (MO); 1250–1350 m, *79018* (CR, INB, MO); *Grayum & French 5820* (MO); *Nilsson et al. 383* (CR); along Camino Raiz de Hule, SE of Platanillo, 1200–1400 m, *Croat 36824* (MO). **Heredia**: 3 mi. S of Cariblanco, 760 m, *Croat 35778* (MO); 4 mi. N of V. Bara Blanca, 1350 m, *Croat 35620* (F, MO, PMA); Río La Paz Grande, 7.5 km N of Vara Blanca, 1270–1350 m, *Croat 36017* (MO); Río Santo Domingo, ca. 3 km E of San Rafael de Vara Blanca, Volcán Barva, 2060–2100 m, 10°11′N, 84°07′W, *Grayum 7333* (CR, MO, US); Volcán Barva, Finca Montreal, Río Volcán–Río San Fernando, 1740 m, 10°12′39″N, 84°06′45″W, *Boyle et al. 1155* (MO, NY); Volcán Barva, along Río Vueltas, 1900 m, 10°06′N, 84°04′W, *Burger & Gentry 9042* (F, US); Parque Nacional Braulio Carrillo, 1000 m, 10°16′38″N, 84°04′57″W, *Boyle 964* (CM, MO, TEX); *1223* (CR, MO); 1990 m, 10°11′03″N, 84°06′27″W, *1058* (CR, MO); 1750 m, 10°03′40″N, 84°01′W, *2432* (CR, MO, NY). **Puntarenas**: Monteverde Reserve, 1500 m, ca. 10°17′N, 84°48′W, *Croat 61194* (CM, MO, PMA); Coto Brus, Cordillera de Talamanca, 730 m, 9°01′30″N, 82°57′40″W, *Mora 14* (INB). **San José**: 4 km N of Cascajal, 7 km N of Las Nubes on CR 216, 1500–1600 m, *Utley & Utley 5259* (DUKE); Cerro de la Muerte, ca. 2000 m, *Croat 32859* (MO); Braulio Carrillo National Park, 1000–1500 m, 10°05′N, 83°57′W, *Croat 61226* (MO). PANAMA. **Bocas del Toro**: Cerro Colorado, 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69066* (CM, CR, MO, PMA); Fortuna Dam area, Chiriquí Grande–Fortuna, 1.2 mi N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat 60447* (CR, MO, NY, PMA, TEX); 0.3 km N of Divide, 970 m, 8°43′N, 82°17′W, *Croat & Zhu 76518* (CR, DUKE, MO, WIS). **Chiriquí**: Cerro Colorado, above San Félix, 18–27 mi. off Pan-American Highway, 1200–1500 m, *Croat 33153* (MO); 20 mi. N of Río San Félix, 2000 m, *Croat 48460* (MO, TEX); 18.5 mi. N of Río San Félix, 1660 m, 8°30′N, 81°46′W, *Croat 74991* (AAU, CAS, CM, COL, CR, G, K, MEXU, MO, QCA, US); Cerro Hornito, above Los Planes de Hornito, 1750–1900 m, 8°41′N, 82°10′W, *Croat 67979* (F, MEXU, MO, PMA); Cerro Pate Macho, NE of Boquete, 1630–1780 m, 8°46′N, 82°25′W, *Croat 66395* (F, MO); 1800–2200 m, *48560* (MO); 1900–2000 m, *66505* (B, CM, COL, CR, DUKE, F, L, MEXU, MO, QCA, TEX, US, VDB, VEN); ca. 2200 m, *Croat 48545* (MO); 1650–2000 m, 8°50′N, 82°25′W, *McPherson 11315* (MO, PMA); Cerro Punta, above town, 2250 m, *Croat 48601* (MO); Fortuna Dam area, Gualaca–Chiriquí Grande, Río Chiriquí, 9.1 mi. beyond Los Planes de Hornito, 1300 m, *Croat 48758* (MO); Quebrada Arena, 1050 m, 8°45′N, 82°16′W, *Hammel et al. 14705* (MO). **Coclé**: El Valle region, La Mesa, N of El Valle de Antón, E edge of Cerro Gaital, 900–1000 m, 8°37′N, 80°08′W, *Croat 67234* (MO, PMA); 900–930 m, *37433* (F, MO); El Copé area, on western slope, just S of the old saw-works area, 700 m, 8°38′N, 80°35′W, *Croat & Zhu 76795* (MO). **Panamá**: Cerro Jefe region, 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan-American Highway, 700–750 m, 9°15′N, 79°25′W, *Croat 68691* (AAU, CAS, K, MO, NY). **Veraguas**: Santa Fe region, Santa Fe–Calovébora, beyond Escuela Agrícola Alto Piedra, beyond Río Tercero Brazo, 600 m, 8°31′N, 81°08′W, *Croat 66930* (CM, MEXU, MO, NY, PMA); Río Primero Brazo, 490 m, 8°33′N, 81°08′W, *66879* (CM, CR, HUA, IBE, JBGP, MO, PMA, QCA, US); ca. 3 mi. N of the school, ca. 700 m, *Croat 49002* (MO); 1.7 mi. past the school, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76832* (MO); slopes of Cerro Tute, near Escuela Agrícola Alto Piedra, 800–1030 m, *Croat & Zhu 76872* (CAS, MO); 1050–1150 m, *Croat 48896* (CM, MO); 0.6 mi. beyond school, 730 m, *Croat & Folsom 33954* (F, MO, PMA); *34041* (MO); Cerro Tute, 1250–1350 m, *Croat 48958* (CAS, MO); 800–950 m, 8°33′N, 81°08′W, *Croat 67002* (CAS, CR, L, MO, NY, PMA).

Philodendron smithii Engl., Bot. Jahrb. Syst. 26: 540. 1899. TYPE: Guatemala. Izabal: Río Dulce at Livingston, sea level, 5°49′N, 88°45′W, *J. D. Smith 1535* (lectotype, here designated, US; isolectotype, K). Figures 364, 372, 373, 377, 378.

Usually hemiepiphytic, sometimes terrestrial or epilithic; stem usually appressed-climbing, leaf scars conspicuous, 7–15 mm long, 7–16 mm wide; internodes glossy, (1)2.2–3 cm long, 2–3 cm diam., usually longer than broad or about as long as broad, tan or gray-green to dark green, epidermis drying yellow-brown with loose flakes, fissured conspicuously; cataphylls soft, spongy, 12–20 cm long, bluntly to sharply 2-ribbed, green, dark green short-lineate, rounded at apex, drying tannish to yellowish, deciduous, intact; **petioles** 21.5–63 cm long, 4–16 mm diam., subterete, spongy, medium green, obtusely flattened with obtuse angle toward apex adaxially, surface dark short-lineate, dark with a dark purple-black ring around apex; **blades** narrowly ovate, subcoriaceous, glossy, moderately bicolorous, acuminate to long-acuminate at apex (the acumen inrolled, 1–4 mm long), cordate at base, 26.5–53 cm long, 11–31 cm wide (1.2–2.2 times

longer than wide), (0.7–1.4 times longer than petiole), margins hyaline, convex is lower half of blade, upper surface dark green, drying dark gray-green to yellow-brown, lower surface light greenish, usually drying yellow-green to yellow-brown, sometimes olive-green; anterior lobe 18–41 cm long, 18–30 cm wide, (1.8–2.9 times longer than posterior lobes); posterior lobes (3.2)7.5–16 cm long, 8.7–14.2 cm wide, obtuse to broadly rounded; midrib flat to broadly convex, paler than surface above, prominently raised, concolorous below; basal veins (3)4–5(6) per side, with 0–1 free to base, 1–2 coalesced (1.8)2.5–5.5(7.5) cm; posterior rib not at all naked or briefly so, usually 1–1.5 cm (rarely to 2 cm); primary lateral veins 3–6 per side, darker than surface below, departing midrib at a 50–70° angle, ± straight, eventually weakly arcuate to the margins, sunken above, convex below; interprimary veins weakly raised, darker than surface below; minor veins numerous, sparsely visible, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2 per axil; peduncle 9–22 cm long, (1)9–12 mm diam., medium green, moderately spongy; **spathe** ± erect, 8.8–19.8 cm long, (0.5–1.4 times longer than peduncle), prominently constricted at anthesis; spathe blade yellowish green to green, glossy outside, 7 cm long, 1.7 cm diam., whitish green, minutely white-dotted, sometimes orange-striate inside; spathe tube ellipsoid, green outside, 8.5 cm long, 2.5 cm diam., light red to maroon (B & K red-purple 2/10) inside; **spadix** stipitate 6–15 mm long; gradually to bluntly tapered to apex, 9.3–16.9 cm long; pistillate portion pale green to greenish yellow, 3.3–5.2 cm long in front, 2.2–2.5 cm long in back, 1.4 cm diam. at apex, 1.3–1.6 cm diam. at middle, 1.6 cm wide at base; staminate portion 6.5–11.3 cm long; fertile staminate portion creamy white, 9–12 mm diam. at base, 1–1.2 cm diam. at middle, 5–7 mm diam. ca. 1 cm from apex, broadest at the middle, narrower than the pistillate and sterile portions; sterile staminate portion broader than the pistillate portion, creamy white, (9)1.1–1.5 cm diam.; pistils 1.8–2.3 mm long, 1.1 mm diam., creamy white; ovary 6–8-locular, 0.9–1.2 mm long, 1 mm diam., usually with basal, somtimes sub-basal placentation; locules 0.9–1.1 mm long, 0.3–0.4 mm diam.; ovule sac 0.9(1.2) mm long; ovules 1 per locule, contained within transparent ovule sac, 0.3–0.4 mm long, about as long as funicle; funicle 0.3–0.4 mm long (can be pulled free to base), style 0.6–0.8 mm long, 1.1 mm diam., similar to style type B; style apex ± sloping; stigma subdiscoid, greenish yellow, 1 mm diam., 0.3 mm high, covering entire style apex; the androecium irregularly 5–6-sided, sometimes oblong or quadrangular, 1.6–1.9 mm long, 0.9–1.2 mm diam. at apex; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another and nearly contiguous; sterile staminate flowers blunt, irregularly 4–6-sided, sometimes prismatic, (1)1.6–2 mm long, (1.2)1.7–1.8 mm wide. Berries white or sometimes yellowish; seeds 1 per locule, tan, oblong, 2 mm long, 0.8 mm diam.

Flowering in *Philodendron smithii* occurs principally in the dry season, and flowers have been collected from December to April (but also July). Post-anthesis collections are common from February through July but with a few in October, November, and December. The latter, especially those in October and November, are the most aberrant, since even if this species is cued to flower by the onset of the dry season (which appears to be the case), they would appear to have flowered too early. This may be explained by the fact that the dry season starts much earlier in Mexico and Guatemala than in Costa Rica and Panama.

Philodendron smithii ranges from Mexico (mostly in Chiapas, Tabasco, and Quintana Roo) to Guatemala, Honduras, and Nicaragua on the Atlantic slope at 40 to 1630 (mostly less than 600) m elevation. It is known from "Selva Alta Perennifolia" and "Selva Mediana Subperennifolia" in Mexico as well as from *Tropical moist forest* and *Subtropical wet forest* in Guatemala.

Philodendron smithii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is characterized by its conspicuously fissured tan internodes, which are about as long as to longer than broad; sharply two-ribbed, deciduous cataphylls; spongy subterete petioles; usually blackish, narrowly ovate-cordate leaf blades; long-pedunculate inflorescences; and externally green spathes that are maroon inside the tube.

Philodendron smithii is not easily confused with any other species in Central America. It is most similar to *P. panamense,* which is endemic to Panama, and shares with that species similarly dark-drying ovate-triangular, long-petiolate blades and long-pedunculate inflorescences. *Philodendron panamense* differs in having much shorter internodes (shorter than broad on flowering plants), weakly one-ribbed cataphylls, moderately firm petioles, and spathes green on the tube outside with a white blade and greenish white throughout within (vs. green throughout outside and maroon on the tube within for *P. smithii*).

Philodendron smithii is also similar to *P. straminicaule* and *P. wilburii,* both from Costa Rica and

Panama and both differing in having stems drying gray-green to grayish or stramineous rather than conspicuously yellow-brown as in *P. smithii.*

Mayo (1986) reported that *P. smithii* lacks superficial resin canals in the spathe and that instead resin production has entirely shifted to the spadix. However, we observed resin canals on the inner surface of both the spathe and the blade in this species.

A noteworthy collection is *Standley 52776* from the Lancetilla Valley in Honduras. It has leaf blades with broadly flaring lobes, but otherwise does not differ from other collections.

One outlying collection in Mexico, from the state of Querétaro at 450 m (*López 539*), is believed also to be this species.

Mayo (1989) reported style type E for *Croat 47913,* but my investigations of flowers of that collection showed no evidence of an annulus on the ovary, and while there was a slight depression in the style apex, the latter was not deemed sufficiently funnel-shaped to qualify for anything except a type B style.

The type specimens (*J. D. Smith 1535*), though unequivocal, were distributed by Engler with a printed label bearing the name *Philodendron donnell-smithii,* but no such name appears in Engler's publications.

Additional specimens examined. BELIZE. Camp 1, flood plain of the Caves Branch River, *Whitefoord 1263* (BM); Sibun River, Gracie Rock, *Gentle 1715* (MICH). **Cayo**: near Camp 6, *Gentle 2424* (CM, MICH). **Stann Creek:** Stann Creek Valley, 250–300 ft., *Schipp S-304* (F, GH, MO); Leoniel Valley, *Gentle 3513* (MICH, NY); Cockscomb Mountains, 2 km N of Victoria Peak, 300–500 ft., *Gentry 8033* (MO). **Toledo**: Richardson Creek, affluent of Bladen Branch, Maya Mountains, 100–250 m, 16°33′N, 88°47′W, *Davidse & Brant 31877* (BM, GH, MO); 80–420 m, 16°32–33′N, 88°45–46′W, *32052* (MO); Richardson Creek–Quebrada de Oro, canyon along Bladen Branch, 100–200 m, 16°31–33′N, 88°46–49′W, *Davidse & Brant 32230* (MO); Columbia Forest Station, 1.5 mi. from Maya village of San José, *Gentry 8132* (MO); *Croat 24360* (MO); *Dwyer 9891* (MO); Southern Mayo Mountains, Bladen Nature Reserve, 400–500 m, 16°30′22″N, 88°54′54″W, *Davidse & Meadows 35827* (BRH, CM, MO, SEL); Big Fall Estate, ca. 3 airline km NE of village of Big Fall, 40 m, 16°16′22″N, 88°52′27″W, *Davidse 35628* (BRH, MO). GUATEMALA. **Alta Verapaz**: Tucurú–El Estor, 9 mi. up road to Oxec, 700 m, *Croat 41652* (MO); 800 m, *41694* (MO); 4 mi. up road to Oxec, 500 m, *41611* (MO); road to El Estor, 5 mi. W of Tucurú, 12 mi. E of Hwy. CA-14 to Cobán, 600 m, *Croat 41512* (MO); Pantín, below Tamahú, ca. 600 m, *Standley 70512* (F); *70513* (F); along Quiché Highway, ca. 12 km W of San Cristóbal, ca. 1100 m, *Standley 89738* (F); near Tactic, ca. 1500 m, *Standley 92022* (F); vic. of Cobán, ca. 1300 m, *Standley 92676* (F); ca. 20 km W of Cobán at Cruz Max, 1500 m, *Castillo & Hodel 1100* (MO); vic. of Cubilgüitz, 1.5–2 mi. S, 300–350 m, *Steyermark 44404* (F, MO); Río Carchá, Cobán–San Pedro Carchá, ca. 1360 m, *Standley 90086* (F); Río Polochic, below Tamahú, ca. 975 m, *Standley 91990* (F). **Baja Verapaz**: Biotopo del Quetzal, 1630 m, *Martínez et al. 23011* (MEXU). **Izabal**: Quiriguá vicinity, 75–225 m, *Standley 23911* (US); ca. 4 mi. SW of Puerto Barrios, 50 m, *Croat 41823* (MO); ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41804* (MO); Lago Izabal vicinity, 0–600 m, 89°0–25′W, 15°15–35′N, *Jones et al. 3046* (F, NY); near Entre Ríos, ca. 18 m, *Standley 72746* (F); Bananera–La Presa, Montaña del Mico, 40–300 m, *Steyermark 38184* (F); Montaña del Mico, between Milla 49.5 and ridge 6 mi. from Izabal, 65–600 m, *Steyermark 38509* (F); *38613* (F). **Petén**: La Libertad, *Lundell 2994* (MICH, US); Uaxactun, *Bartlett 12426* (MICH, UC, US); El Paso, *Lundell 1572* (CM, MICH); *2929* (MICH); Santa Teresa, *Lundell 2888* (GH, MICH); Tikal National Park, 2 mi. S of entrance, 500 ft., *Croat 24700* (MO); Finca Yalpemech, Río San Diego, 50–150 m, *Steyermark 45315* (CM, F, NY, US). **Zacapa**: 41 mi. S of turnoff to Petén Morales, 150 m, *Croat 41874* (MO). HONDURAS. Potrero, along Highland Creek, *Wilson 484* (NY). **Atlántida**: San Alejo vicinity, near Río San Alejo, 150–270 m, *Standley 7699* (F); San José de Texíguat, SE of Tela, *Nelson 10732* (TEFH); Lancetilla Reserve, ca. 2 mi. WSW of Tela and S of main hwy., 70–90 m, 15°44′N, 87°27′W, *Croat & Hannon 64588* (CM, F, K, MO, US); 100 m, *Molina & Molina 25650* (EAP, F, NY); 20–600 m, *Standley 52776* (F, US); 20–600 m, *Standley 52980* (F, US); 45 m, *Allen 6143* (EAP, F); 10–150 m, *Croat 42656* (MO), *42675* (MO); 19.2 km E of Tela on Tela–Ceiba Highway, near San Francisco de Soco, 50–100 m, 15°44′N, 87°21′W, *Brant & Zúñiga 2845* (EAP, MO, US); Campamento Quebrada Grande, ca. 10 km SW of La Ceiba, 80–180 m, 15°42′N, 86°51′W, *Liesner 26179A* (MO). **Cortés**: Lago de Yojoa, 650 m, *Croat 42761* (MO); Agua Azul, *Allen 6448* (EAP, F). **Lempira**: Montaña de Celaque, between Gracias and top of Cerro Celaque, 14°33′N, 88°39′W, *Davidse & Zúñiga 34540* (MO). **Olancho**: Río Wampusito, Dulce Nombre de Cuimí, 500–700 m, 15°15′N, 85°25′W, *Nelson & Clewell 439* (EAP, FSU, MO); San Esteban–Bonito Oriental, Río Grande, 3.3 mi. SW of border with Colón Dept., 350–400 m, 15°31′N, 85°42′W, *Croat 64524* (AAU, CAS, EAP, GB, K, MEXU, MO, NY, P). MEXICO. **Chiapas**: Mpio. La Trinitaria, Lagos de Montebello National Park, at Cinco Lagunas, 1600 m, *Breedlove 68620* (CAS); 10 km ENE of Dos Lagos, above Santa Elena, 1170 m, *Breedlove & Almeda 57585* (MO); 1000 m, *Breedlove 56538* (CAS); Mpio. Las Margaritas, confluence of Río Ixcán and Río Lacantum, 300 m, *Breedlove & McClintock 34198* (MO); 12 km E of Tziscao, 1200–1300 m, *Davidse et al. 29886* (MO); Palenque–Boca Lacantum, Mpio. Ocosingo, Nuevo Guerrero, 340 m, *Martínez 18108* (MO); Ojo de Agua de San Javier, a 23 km al SE de Nuevo Guerrero, road to Boca Lacantum, 370 m, *Martínez 16929* (MO); 2 km N of Naja, trail to Chancala, 900 m, *Martínez 21320* (MEXU), *21328* (MEXU), *21331* (MEXU); San Cristóbal–Palenque, San Cristóbal de las Casas, 97 km NE of San Cristóbal, 1130 m, 17°27′N, 92°04′W, *Hammel et al. 15625* (K, MEXU); 70 km SW of Palenque, *Breedlove 47180* (CAS, MO); Laguna Ocotalito, 12 km N of Monte Líbano, trail to Chancala, 950 m, *Martínez 17605* (MO); near lake at Naja, 300 m, *Breedlove 49951* (CAS); Mpio. Pueblo Nuevo Solistahucán, 3 km NW of town, 6700 ft., 17°30′N, 92°40′W, *Will 412* (CAS, DH); San Fernando–Maravillas, 840–940 m, 16°53′N, 93°16′W, *Croat & Hannon 65003* (COL, F, K, MEXU, MO, NY, US); 20–30 mi. SW of El Jocote, road to Motozintla de Mendoza, 700–900 m, *Croat 40707* (B,

MEXU, MO); 1 mi. N of Escuintla, 100 m, *Croat 43802* (MO); 200 m, *Croat 40134* (MO); 160 m, *40295* (B, K, MEXU, MO); 210 m, *Croat 40317* (MO); 1000 m, *Croat 40588* (MO); 700 m, *Croat 40660* (B, MEXU, MO); 550 m, *Breedlove 56538* (CAS); ca. 400 m, *Croat 40190* (MO, NY); 460 m, *40271* (MO); 350–370 m, *40223* (MO); 0.6 mi. N of Tapulula, 35.6 mi. SSE of Pichucalco, 750 m, 17°16′N, 93°01′W, *Croat & Hannon 65285* (B, MO); 8 mi. N of Pichucalco, 80 m, *Croat 40079* (CM, L, MEXU, MO, PMA, US). **Oaxaca**: Uxpanapas region near Sarabia, 52 km E of main highway, 100 m, 17°10′N, 94°32′W, *Hammel & Mer-ello 15579* (MEXU, MO); Chiltepec, 30 m, *Sousa 1732* (MEXU). **Queretaro**: Mpio. Jalpan, Río Las Paguas, S of Tanchanaquito, 450 m, *López 539* (MO). **Quintana Roo**: 110 km SW of Chetumal, 100 m, *Davidse et al. 20172* (MEXU, MO). **Tabasco**: 3.1 mi. E of Teapa, 150 m, 17°33′N, 92°59′W, *Croat & Hannon 65364* (MO); ca. 9 km E of Teapa, cultivated, *Mayo 85* (K, MO); base of Cerro de Madrugal, ca. km 4 SE of Teapa, 40 m, *Croat 40133* (MO); ca. 300 m, *47913* (CM, G, MEXU, MO, US); Mpio. Macuspana, Centro Recreativo de Agua Blanca, 7 km from the Villahermosa–Escarcega Highway, *Cowan & Zamudio 3351* (CAS, MEXU, MO, NY); Mpio. Tacotalpa, 0.2 km NW of Tapijulapa, *Cowan et al. 3530* (CSAT). NICARAGUA. **Jinotega**: Jinotega–Matagalpa, ca. 5–8 mi. SW of Jinotega, 1500 m, *Croat 43059* (MO). **Río San Juan**: Río Santa Cruz–Caño Santa Crucita, La Palma, 40–60 m, 11°2–4′N, 84°24–26′W, *Stevens 23432* (MO). **Zelaya**: Caño Monte Cristo, vic. Campamento Germán Pomares, ca. 10 m, 13°35′N, 83°51′W, *Moreno 14841* (MO); Cerro La Calera, 4 km N of Siuna, 350 m, *Neill 4290* (BM, MO); Cerro Waylawás, ca. 100–268 m, 13°39′N, 84°48–49′W, *Stevens 7380* (MO); ca. 80 m, ca. 13°39′N, 84°49′W, *Pipoly 4406* (MO).

Philodendron sousae Croat, sp. nov. TYPE: Mexico. Chiapas: Mpio. Ocosingo, Río Santo Domingo at Santo Domingo, 490 m, *Davidse et al. 20450* (holotype, MO–2946607; isotype, MEXU). Figures 379, 380.

Planta hemiepiphytica; internodia usque 3.5 cm longa, 8–15 mm diam.; cataphylla incostata, decidua; petiolus semiteres, 29–54 cm longus, 8–12 mm diam.; lamina ovato-cordata, 28–55 cm longa, 12.5–28 cm lata, in sicco brunnea vel olivacea supra, virella vel flavibrunnea infra; nervis lateralibus I 3–4; inflorescentia usque 4; spatha 15–21 cm longa, lamina spathae extus cremea, tubo spathae albo, in superficiebus ambabus saturate suffuso rubro aut purpureo; pistilla 6–8-locularia; loculi 2-ovulati.

Hemiepiphytic; stem probably scandent; internodes to 3.5 cm long, 8–15 mm diam., yellow-brown to dark brown, epidermis drying smooth to wrinkled, sometimes fissured closely; roots drying reddish brown, thin, elongate, drying 3–4 mm diam., few per node; cataphylls 14 cm long, unribbed, deciduous; **petioles** 29–54 cm long, 8–12 mm diam., ± terete, drying yellow-brown; sheathing 3–6.5 cm; **blades** ovate-cordate, subcoriaceous, gradually acuminate at apex, conspicuously cordate at base, 28–55 cm long, 12.5–28 cm wide (2.2 times longer than wide), (about as long as petiole), drying subcoriaceous, upper surface drying brown to olive-green, lower surface drying greenish to yellowish brown, smooth or minutely ridged; anterior lobe 23–36 cm long, 21–27 cm wide (2.8–3 times longer than posterior lobes); posterior lobes 8–12 cm long, 10–13 cm wide; sinus parabolic; midrib drying broadly convex and usually paler than surface above, drying narrowly convex and usually concolorous below; basal veins 3–5 per side, free to base, several coalesced to 1–2 cm, occasionally 2 fused to 3.5 cm; posterior rib usually not at all naked, sometimes obscurely so for about 1 cm; primary lateral veins 3–4 per side, departing midrib at a 60–70° angle, weakly arcuate to the margins, drying weakly raised and usually paler than surface above, drying raised below; minor veins arising from both the midrib and primary lateral veins. INFLORESCENCES to 4 per axil; peduncle 6.5–13 cm long, ca. 1 cm diam.; **spathe** 15–21 cm long (1.6–2.3 times longer than peduncle), with resin canals on inner surface, visibly constricted above the tube; spathe blade cream outside; spathe tube white, heavily tinged red or purple on both surfaces, spathe tube 5–11 cm long; **spadix** sessile; 6–14 cm long; pistillate portion cylindrical-tapered toward the apex, 2.4–4.1 cm long, 4–9 mm diam. at apex, 5–10 mm diam. at middle, 6–10 mm wide at base; staminate portion 3.6–10 cm long; fertile staminate portion (4)9 mm diam. at base, 6–12 mm diam. at middle, 3–7 mm diam. ca. 1 cm from apex, broadest at or below middle, broader than the pistillate portion; sterile staminate portion not obvious; pistils 0.5–2.7 mm long, (0.7)1.8–2.7 mm diam.; ovary 6–8-locular, 0.4–1.4 mm long, 0.7–2.7 mm diam., with basal (to sub-basal) placentation; locules 0.4–1.4 mm long, 0.9 mm diam.; ovule sac 0.3 mm long; ovules 2 per locule, contained within a translucent, gelatinous ovule sac, 0.1–0.2 mm long, much shorter than funicle; funicle 0.7–0.9 mm long, style 0.4 mm long, 0.4–1.5 mm diam., similar to style type D; stylar canals emerging at base of apical depressions and arranged separately in a ring on orifices around center; style apex flat; style boss moderately shallow to moderately prominent; stigma discoid, 0.4 mm diam., 0.1 mm high, covering entire style apex; thecae oblong to weakly ovate, 0.2–0.4 mm wide, divaricate.

Flowering in *Philodendron sousae* occurs in the early rainy season, and specimens have been collected in May and August. Fruits are not known.

Philodendron sousae is endemic to Mexico in Chiapas, at 490 to 1400 m elevation on the Atlantic slope in regions of "Selva Alta Perennifolia."

Philodendron sousae is a member of *P.* sect. *Ca-*

lostigma subsect. *Macrobelium* ser. *Macrobelium.* This species is characterized by its ovate-cordate, light greenish-brown-drying blades with three to four primary lateral veins per side and three to five free to weakly coalesced basal veins, which are usually not at all naked. Also characteristic are the inflorescences, ranging up to four per axil and with the spathe more or less oblong and constricted somewhat above the tube. The spathe tube is white and heavily tinged with red or purple on both surfaces.

Philodendron sousae is most easily confused with some material of *P. advena* (from the Pacific slope), which dries a similar light brown to greenish brown (not dark brown typical of most material). The latter differs in having a more or less ellipsoid spathe, scarcely or not at all constricted above the tube.

Philodendron sousae may also be confused with *P. breedlovei,* which has somewhat similar blades that dry a similar color. The latter species has narrower blades, to 1.8 cm long, a single inflorescence per axil, and about 20 ovules per locule (vs. blades usually broadly ovate, averaging 1.4 times longer than wide, four inflorescences per axil, and 1–3 ovules per locule).

Philodendron sousae was first collected by D. E. Breedlove in 1972. It is named in honor of Mario Sousa (MEXU), co-editor of *Flora Mesoamericana* (Davidse et al., 1995), who (in the company of Gerrit Davidse) collected the type specimen.

Additional specimens examined. MEXICO. **Chiapas**: Mpio. Cintalapa: 4 km W of La Ciénega, 38 km W of Las Cruces, Oaxaca–Chiapas border, 1400 m, *Breedlove 25142* (DS); Mpio. Ocosingo, vic. Centro de Población Velasco Suárez (Selva Lacandona), 570 m, 16°47′N, 91°17′W, *Calzada et al. 744* (MO); Laguna Ocotal Grande, ca. 25–30 km SE of Monte Líbano (ca. 45 km E of Ocosingo), 950 m, *Dressler 1589* (GH).

Philodendron squamicaule Croat & Grayum, sp. nov. TYPE: Panama. Coclé: vic. El Copé, on western slope, just S of the old saw-works area, 700 m, 8°38′N, 80°35′W, 12 July 1994, *Croat & Zhu 76798* (holotype, MO–4613255–8; isotypes, B, CAS, CM, COL, CR, F, G, K, MEXU, NY, PMA, US, VEN). Figures 374, 381–384.

Planta hemiepiphytica; internodia brevia, 1–8 cm longa, 2–3.5 cm diam., dense squamata; cataphylla 27–34 cm longa, incostata, rosea vel rubella aut rubribrunnea, persistentia semi-intacta; petiolus teres vel subteres, 28–61 cm longus, 1 cm diam., dense squamatus, squamae purpurascentes; lamina ovato-triangularis, 26–53 cm longa, 17.5–40 cm lata, sagittato-cordata basi; nervis lateralibus I dense puberulis infra; inflorescentia usque 5; pedunculus 3.5–8 cm longus, olivaceus, dense squamatus; spatha 15–17 cm longa; lamina spathae extus viridalba, intus diluta viridi, suffusa rubra, dense squamata; tubo spathae omnino viridi, suffuso rubro; pistilla (3)4(5)-locularia; loculi 20–28-ovulati.

Hemiepiphytic; appressed-climbing, stem 3–20 cm long; internodes short, densely scaly with ± deltoid, sometimes bifurcated scales, mixed with fewer acicular scales, drying reddish brown, 1–8 cm long, 2–3.5 cm diam., longer than broad, semiglossy, dark green, soon gray-green, finally tannish to brownish, drying straw-colored to reddish brown to brown, completely hidden by old cataphylls; roots few per node, slender, drying brownish; cataphylls fleshy, 27–34 cm long, unribbed to bluntly 2-ribbed, yellow-green, pink to reddish, or reddish brown, densely long-scaly throughout with a sparse underlay of tuberculate structures, drying reddish brown, persisting as semi-intact pale fibers, sometimes with patches of epidermis, soon deciduous; margins folded in to form groove. LEAVES erect-spreading; **petioles** 28–61 cm long, ca. 1 cm diam., erect-spreading, terete to subterete, purplish to dark brown, surface densely scaly, 1.5–4 mm long, flattened, with a sparse underlay of tubercules; sheathing briefly only near or at the base; petiolar scales of two types, short purplish scales deltoid or broader than high, less than 0.2 mm high, these interspersed with much longer, spreading light green acicular scales, 3–5 mm long, both types of scales drying reddish brown; **blades** ovate-triangular, thinly coriaceous to subcoriaceous, conspicuously bicolorous, short acuminate to acute at apex, sagittate-cordate at base, 26–53 cm long, 17.5–40 cm wide (1–1.5 times longer than wide), (0.7–1.1 times longer than petiole), broadest at the petiole attachment, margins hyaline, upper surface medium to dark green, semiglossy to sometimes almost matte above, slightly paler, light to silvery-green, glossy to semiglossy below, drying reddish brown on both surfaces; sometimes with sparse whitish raphide cells; anterior lobe 21–28 cm long, 18–26 cm wide (2.2–2.8 times longer than posterior lobes), margins straight to weakly concave; posterior lobes 8–10.7 cm long, 7.1–11.5 cm wide, directed toward the base to somewhat outward, broadly rounded; sinus parabolic to hippocrepiform on younger leaves, mitered on older leaves, 3.5–17 cm deep; midrib flat to sunken or deeply sunken and concolorous above, convex to broadly round-raised, concolorous to paler to light reddish below; basal veins 5–12 per side, with 0(1) free to base, third and higher order veins coalesced 2–6 cm long; posterior rib naked for 3–4.5 cm, densely scaly on both upper and lower edges; primary lateral veins 5–9 per side, departing midrib at a 30–45° angle (55° angle near base), moderately straight to the margins

(the lowermost veins somewhat branched near the margins), deeply sunken and concolorous above, brown to reddish, round-raised and densely puberulent below; tertiary veins visible, slightly raised, darker than surface; minor veins moderately distinct below, arising from both the midrib and primary lateral veins; "cross-veins" sometimes moderately distinct on lower surfaces on drying. INFLORESCENCES to 5 per axil; peduncle 3.5–8 cm long, olive-green, densely scaly, especially near apex, peduncle and spathe with scales of 2 lengths, both long and acicular, 1–2 mm long, much shorter and broader deltoid to tuberculate; **spathe** 15–17 cm long, 2–4.8 times longer than peduncle, moderately constricted above the tube, green, densely to sparsely scaly outside, shortly acuminate at apex; spathe blade sometimes greenish white outside, to 5.5 cm diam., light green, tinged red near base inside; spathe tube ± ellipsoid, green, tinged red, covered with greenish scales (except for 5 mm along margin to 3 cm along infolded edge near base) outside, ca. 6 cm long, to 3.5 cm diam., reddish violet inside except greenish near tip inside; **spadix** 13.2 cm long; pistillate portion pale green to dirty-white, to 4.2 cm long in front, 3.6 cm long in back, 12 mm diam. at apex, 14 mm diam. at middle; staminate portion 11.5 cm long; fertile staminate portion 1.2 cm diam. at base, 1 cm diam. at middle, 7 mm diam. ca. 1 cm from apex; sterile staminate portion 1.2 cm diam.; pistils 1.22 mm diam.; ovary (3)4(5)-locular, with axile placentation; locules 1–1.2 mm long; ovules 20–28 per locule, 2-seriate, ca. 0.2 mm long, longer than funicle; style similar to style type D; style apex flat; style boss narrow, fairly shallow; stigma hemispheroid, 0.7–0.8 mm diam., 0.2 mm high; the androecium prismatic, margins irregularly 4–6-sided, 1.4–1.6 mm long, 1.4–1.6 mm diam.; sterile staminate flowers prismatic, margins irregularly 4–6-sided, 1.1–1.2 mm diam. INFRUCTESCENCE with peduncle to 11 cm long, 8–11 mm diam.; spathe to 23 cm long, 1.7 cm diam., dark punctate in part and drying light brown inside; spathe tube 9–9.5 cm long, reddish, spathe blade to 14 cm long; spadix to 21 cm long; pistillate spadix 6–8.5 cm long, 3.2 cm wide; pistils 4.2 mm long, 2.7 mm diam.; locules to 3.3 mm long; fertile staminate spadix 11.5 cm long, 1.1 cm diam. midway; sterile staminate spadix 2.5 cm long, 1.4 cm diam.; staminate flowers to 3.3 mm long; berries white; seeds to 18 per locule, 1 mm long. JUVENILE plants terrestrial, scandent; lower surface of blades purplish violet. PREADULT plants with internodes 2–30 cm long, 0.5–1.2 cm diam.; petioles 8.5–18.5 cm long, 2–3 mm diam.; blades 14–28 cm long, 15–22 cm wide.

Flowering in *Philodendron squamicaule* occurs in the early rainy season from May through August. Mature fruits have been collected in early December.

Philodendron squamicaule ranges from Costa Rica to Esmeraldas Province, Ecuador, from <100 to 1250 m elevation in pluvial forest, *Premontane wet forest,* and *Premontane rain forest* life zones. In Central America it has not been collected below 550 m elevation.

Philodendron squamicaule is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is recognized by its appressed-climbing habit, moderately thin, triangular-ovate, semiglossy blades, and especially by its scaly stems, cataphylls, petioles, peduncles, and outer surfaces of spathes and densely puberulent major veins on the lower blade surface.

Philodendron squamicaule is apparently closest to *P. serpens* Hook. f., which was described from a cultivated plant from an unknown Colombian locality. The latter species differs in having oblong-ovate blades, sometimes with a constriction above the posterior lobes, with 4–5 basal veins on the most well developed blades (in contrast to 6–12 basal veins). In addition, *P. squamicaule* has a coarse row of scales extending along both edges of the posterior rib and densely puberulent primary lateral veins, neither of which was described for *P. serpens. Philodendron serpens* also differs in having glabrous, rather than scaly, peduncles and spathes.

Philodendron squamicaule is probably related to *P. verrucosum,* which also has densely scaly petioles. That species differs, however, in having longer petioles (more than 30 cm long vs. less than 30 cm for *P. squamicaule*), and broadly ovate blades that are velvety and matte above and matte with frequently purplish areas along the veins below (vs. usually solid green below in *P. squamicaule*). Both species have a similar number of primary lateral veins, but the veins are much more closely spaced in *P. squamicaule* than *P. verrucosum.*

Additional specimens examined. COSTA RICA. **Heredia**: N of Quebrada Tigre, from Finca El Plástico (ca. 8 km SW of Las Horquetas), 450–550 m, 10°18′N, 84°02′W, *Grayum & Sleeper 6523* (CR, MO, US); Zona Protectora, between Río Peje and Río Gúacimo, Volcán Barba, 750 m, *Grayum & Schatz 3250* (DUKE); Sarapiquí, P. N. Braulio Carrillo, El Ceibo, 750 m, 10°17′50″N, 84°04′25″W, *Boyle et al. 2897* (CR, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 4.3 km N of the Continental Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60197* (K, MO, PMA). **Coclé**: 5–5.5 mi. N of El Copé, 850 m, 8°38′N, 80°35′W, *Thompson 4731* (CM); 680–770 m, 8°39′N, 80°36′W, *Croat 74836* (MO, PMA, US); 710–800 m, *68764* (MO, NY).

Veraguas: Alto Piedra–Calovébora, 0.5 mi. N of Alto Piedra, Parque Nacional Cerro Tute, 800–1030 m, *Croat & Zhu 76906* (CR, MO, NY); ca. 5 mi. N of Alto Piedra, 670 m, 8°33′N, 81°08′W, *Croat 66962* (CM, F, MO); 1250–1350 m, *Croat 48959* (MO).

COLOMBIA. **Chocó**: between Medellín and Quibdó, 60 km W of Bolívar, 800 m, *Croat 49271* (MO); 5.5 km E of Tutunendo, 23.5 km E of Quibdó, 150 m, 5°44′N, 76°29′W, *Croat 56227* (COL, JAUM, MO); km 208.5, 9 km W of Tutunendo, ca. 9 km E of Quibdó, <100 m, 5°39′N, 76°40′W, *Croat 56204* (COL, JAUM, MO); Quibdó–Bolívar, Km 175–176, 117–118 km E of Quibdó, 5°44′N, 76°20′W, *Croat 57481* (CHOCO, COL, MO); Quibdó–Lloro, vic. Río Atrato, ca. 150 m, 5°29′N, 76°35′W, *Croat 55996* (COL, JAUM, MO, PMA). **Valle**: Buenaventura–Cali, 14 km SE of Río Sabaletas, 53 km ESE of Queremal, 270, 3°42′N, 77°51′W, *Croat & Watt 70458* (MO). ECUADOR. **Esmeraldas:** Lita–San Lorenzo road (based on *Dodson 18645*), cultivated at Río Palenque, *Croat 73857* (MO).

Philodendron squamipetiolatum Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario above El Copé, ca. 6 mi. N of El Copé, 710–800 m, 8°39′N, 80°36′W, 23 June 1994, *Croat 68767* (holotype, MO–3591312–4; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, G, GH, HMNM, K, M, MEXU, NY, PMA, RSA, S, SCZ, TEX, US, VEN). Figures 375, 385–388.

Planta hemiepiphytica; internodia 3–17 cm longa, 6–15 mm diam., atriviridis, squamis approximatis, scalariformibus, caespitosis, transverse orientibus; cataphylla usque 29 cm longa, incostata, squamata, persistentia nodis superioribus, mox decidua; petiolus 6–16 cm longus, usque ca. 6 mm diam., teres; lamina ovata, rotundata vel subcordata basi, 15–37.5 cm longa, 9.5–29 cm lata; inflorescentia 1–2; peduculus subteres, 6–8 cm longus, dense squamatus; spatha 11–15.5 cm longa, 2–2.5 cm diam.; lamina spathae extus viridi, dense squamata, intus atrirubello, tubo spathae extus viridi, intus atrirubello; pistilla 5–6-locularia; loculi 20–30-ovulati.

Appressed-climbing hemiepiphyte, occurring on understory trees in primary forest, fertile ca. 6 cm above the ground; stems trailing when juvenile, loosely appressed-climbing as adults; internodes 3–17 cm long, 6–15 mm diam., dark green, soon dark brown, drying yellow-brown, closely ridged-fissured with the surface moderately glossy, granular and with close, scalariform, tufted transversely oriented scales; cataphylls to 29 cm long, terete, unribbed, green and densely whitish scaly, promptly weathering to a loose semiorganized network of slender, pale fibers with fragments of epidermis, the fibers persisting at upper nodes, but soon completely deciduous; **petioles** erect to spreading, 6–16 cm long, to ca. 6 mm diam., terete, matte, dark green, surface densely covered with antrorse light green scales throughout (these ca. 6 mm long), densely granular-scurfy; **blades** somewhat pendent when young, spreading with petioles when mature, ovate, subcoriaceous, acuminate at apex, rounded to subcordate at base, 15–37.5 cm long, 9.5–29 cm wide (ca. 1.2–2.1 times longer than wide), (1.6–2.3 times longer than petiole), upper surface dark green, weakly glossy (subvelvety), drying dark brown, lower surface matte and much paler, drying yellow-brown; posterior lobes broadly rounded; sinus arcuate; midrib narrowly sunken and paler above, round-raised to thicker than broad, darker and densely puberulent below; basal veins 2–6(9) per side, with all free to base, or sometimes 3–5 pairs coalesced up to 1.5 cm, posterior rib sometimes lacking; primary lateral veins 5–7 per side, departing midrib at a 50–55° angle, weakly quilt-sunken above, round-raised to thicker than broad, darker and densely puberulent below; minor veins flat but distinct and darker than surface below, some intermittent; "cross-veins" distinct, moderately raised on drying. INFLORESCENCES 1–2 per axil; peduncle subterete, 6–8 cm long, densely scaly; **spathe** 11–15.5 cm long, 2–2.5 cm diam. when furled, to 6.5 cm wide, and constricted somewhat when flattened, green outside, especially below, densely scaly (the scales whitish), deep reddish inside, especially in the tube; **spadix** yellowish white, 9.7–13.5 cm long, to 1.3 cm diam., only weakly constricted midway; pistillate portion 2.7–4.7 cm long in the front, 0.7–1.4 cm diam.; staminate portion 7–8.8 cm long; fertile staminate portion broadest at upper one-third and bluntly pointed at apex, 6 mm diam. 1 cm from apex; sterile staminate portion 1.2 cm diam.; pistils 2.2 mm long; ovary 5–6-locular, ca. 1.4 mm long, with axile placentation, the sides covered throughout, especially toward apex, with short pale raphide cells; locules 1–1.2 mm long; ovules 20–30 per locule, 0.1–0.2 mm long, oblong, arranged all along the length of the locules; style similar to style type B; short, 0.9–1 mm diam., drying with 2–5 depressions at apex; stigma 1–1.1 mm diam. when flattened and dried. Infructescence not seen.

Flowering in *Philodendron squamipetiolatum* occurs in the rainy season, during June in Central America. Ecuadorian collections at post-anthesis have been seen from February and April, with an early fruiting collection from August.

Philodendron squamipetiolatum ranges from Panama to Ecuador from sea level to 1300 m elevation in *Premontane rain forest* and *Premontante wet forest* transition to *rain forest* and *Tropical rain forest.* In Panama this species is known only from along the Continental Divide in Coclé Province,

whereas in South America it occurs along the Pacific slope of the Andes.

Philodendron squamipetiolatum is a member of *P.* sect. *Philodendron* subsect. *Achyropodium*. This species is distinguished by its long, inconspicuously scaly internodes; long, scaly, terete petioles (hence the name); long, scaly, deciduous cataphylls; rounded to subcordate blades with an arcuate sinus and puberulent major veins below; 1–2 dark green, scaly inflorescences; and spathe tube reddish within.

In Central America, *Philodendron squamipetiolatum* is most easily confused with *P. hammelii*, a species with which it occurs in the vicinity of the type locality. Both species have small, ovate-cordate blades with scaly petioles and persistent, fibrous cataphylls. *Philodendron hammelii* is distinguished by having leaves drying grayish green above and yellowish brown below and closely arranged broad scales only near the apex of the petioles.

This species might also be confused with two others with scaly petioles. It is easily distinguished from both *P. verrucosum* and *P. squamicaule* by its much smaller, subcordate vs. deeply cordate leaf bases, and from *P. squamicaule* by its more broadly ovate blades (vs. triangular ovate).

Madison & Besse 17185 from Esmeraldas Province, Ecuador, probably also belongs to this species, but field notes indicate that the stems are smooth. Unfortunately, there is no stem with the collection. It is not known whether the intent was to indicate that the stems lacked scales or whether it lacked other features. In addition, the stems were reported to be 10–14 cm long and to 1.5 cm diam.

Additional specimens examined. PANAMA. **Coclé**: Alto Calvario, ca. 4.6 km above El Copé, 800 m, 8°39′N, 80°36′W, *Croat 74857* (AAU, B, CAS, CM, COL, DUKE, F, G, GH, HMNM, K, M, MEXU, MO, NY, PMA, RSA, SCZ, S, TEX, US, VEN); *75098* (MO). **Colón**: Río Guanche, 30–100 m, *Croat 79327* (PMA, MO), *79350* (PMA, SCZ).

COLOMBIA. **Chocó**: Serranía de Baudó, Las Animas–Pato on Río Pato, ca. 4 km SW of Pato, ca. 150 m, 5°30′N, 76°46′W, *Croat 56140* (MO); Serranía de Baudó, Río Pato, 10 km SW of Pato, 5°17′N, 76°45′W, *Croat 56074* (MO); San José del Palmar–Novita, ca. 3 km W of San José del Palmar, 930 m, 4°56′N, 76°29′W, *Croat 56650* (COL, JAUM, MO); Pueblo Rico–Istmina, along Quebrada Antón, 15 km W of Santa Cecila, 240–350 m, 5°20′30″N, 76°13′45″W, *Croat 70972* (MO); 300 m downstream and across the river from Catrú, 50–100 m, *Warner & White 123* (COL). **Valle**: Buenaventura–Cali, Sabaletas, km 29, 25 m, *Killip & Cuatrecasas 38775* (US); 100 m, *Croat 38567* (F, MO); vic. Bajo Calima, <100 m, 4°03′N, 77°08′W, *Croat 70218* (CM, MO, NY); 100 m, *Monsalve 3193* (MO). ECUADOR. **Carchi**: El Pailón, ca. 45 km below Maldonado, 800 m, *Madison & Besse 7185* (SEL); Tulcán Cantón, Awá Reservation, Gualpí Chico area, 1300 m, 0°58′N, 78°16′W, *Hoover et al. 3710* (MO, QCA). **Esmeraldas**: Lita, 550–650 m, *Madison et al. 5057* (SEL); Cerro de Río Bravo de Cayapas, 250 m, 0°41′N, 78°56′W, *Holm-Nielsen et al. 25535* (AAU); 40.1 km W of Lita, 350 m, 0°56′N, 78°40′W, *Croat 72309* (L, MO, QCA, US). **Imbabura**: Lita, 812 m, *D'Arcy 14850* (MO). **Pichincha**: Reserva ENDESA, 9 km N of Km 113 on Quito–Pto. Quito Highway, 750–800 m, 0°05′N, 79°02′W, *Rodríguez 247* (MO, QCA); *Croat & Rodríguez 61483* (MO, QCA); 650–800 m, 0°03′N, 79°07′W, *Cerón & Ayala 10169* (MO); along tributary of Río Guayllabamba, 600 m, 0°10′N, 79°03′W, *Grayum et al. 9353* (MO). **Los Ríos**: La Centinela at Km 12, N of Patricia Pilar, 600 m, *Dodson & Dodson 6771* (MO, SEL); Río Verde, 2 km SE of Sto. Domingo de Los Colorados, 530 m, *Dodson 7435* (SEL).

Philodendron straminicaule Croat, sp. nov. TYPE: Panama. Chiriquí: Fortuna Dam area, trail to meteorological station of Río Hornito, ca. 0.5 km S of Centro de Científicos, 8°45′N, 82°18′W, 23 June 1994, *Croat & Zhu 76302* (holotype, MO–4610957–9; isotypes, AAU, B, CAS, COL, CR, F, GH, K, M, MEXU, NY, PMA, QCNE, S, SEL, US, VEN). Figures 6, 376, 389–392.

Planta hemiepiphytica; internodia 1.5–5(12) cm longa, 2–3.5 cm diam., plus minusve fragilia, canoviridia vel atriviridia, in sicco straminea; cataphylla (17)20–35 cm longa, decidua; petiolus subteres, (27)32–59 cm longus, 5–12(17) mm diam.; lamina triangulari-ovato-cordata, (27)33–55 cm longa, (11)19.7–31 cm lata, cordata basi; inflorescentia 2–3(5); pedunculus (4.5)5.6–18 cm longus; spatha 7–18.5 cm longa; lamina spathae alba in superficiebus ambabus; tubo spathae extus pallide viridi, intus rubroviolaceo vel marronino; pistilla 4–6(10)-locularia; loculi 1-ovulati; baccae virella-albae vel lavandulae.

Hemiepiphytic; stem appressed-climbing, leaf scars conspicuous, 1–1.6 cm long, 1.2–1.7 cm wide; internodes glossy to semiglossy, ± brittle, somewhat scurfy, 1–5(12) cm long, 2–3.5 mm diam., longer than broad, dark green, soon gray-green, finally light tan, drying straw-colored, sometimes with a narrow ring of yellow-brown periderm at the nodes; epidermis transversely fissured in part, sometimes deeply fissured and cracking free on drying; roots blunt, to 30 cm or longer, 4 mm diam., yellow-green, weakly glossy (fresh), drying reddish brown with minute scales in age; cataphylls somewhat spongy, to (17)20–35 cm long, variously ribbed, sometimes D-shaped or unribbed, more frequently bluntly to sharply 1- or 2-ribbed (sometimes unribbed in Coclé), emarginate at apex, pale green to pale yellowish to whitish, margins clear, sometimes closely dark green short-lineate, sometimes moderately red-purple-spotted (more so at base) throughout, ribs darker, drying greenish or brownish, deciduous, persisting intact; **petioles** (27)32–59 cm long, 5–12(17) mm diam., subterete,

± spongy, medium green, obtusely flattened adaxially, rounded abaxially, surface semiglossy, faintly dark lineate; **blades** triangular-ovate-cordate, subcoriaceous, semiglossy, bicolorous, long acuminate at apex, cordate at base, (27)33–55 cm long, (11)19.7–31 cm wide (1.3–2.3 times longer than wide), (0.7–1.5 times longer than petiole), margins hyaline, lower surface drying green to yellow-green, densely glaucous with secretory ducts visible; anterior lobe (18.7)27–38.6(47) cm long, 17.6–27.6 cm wide (2.4–4.5 times longer than posterior lobes), margins straight to moderately concave; posterior lobes directed toward base, rarely reflexed-spreading, sometimes overlapping when posterior lobes are held somewhat upward at an angle to the midrib, (7)8.5–15.5 cm long, 7.5–13 cm wide, obtuse to rounded; sinus hippocrepiform, rarely closed, 2.6–14 cm deep; midrib flat to broadly rounded, paler than surface above, convex to narrowly rounded, paler than surface below; basal veins 4–6(7) per side, with 0–1 free to base, the remainder coalesced 1.2–5 cm, 2 coalesced 3.5–7 cm; posterior rib naked 0.5–1.5 cm; primary lateral veins 3–6 per side, departing midrib at a 45–65° angle, acutely ascending then weakly arcuate to straight to the margins, ± obscure, sunken and concolorous above, convex, darker than surface or paler than surface below; interprimary veins raised and darker than surface below; minor veins moderately distinct, fine, darker than surface, arising from both the midrib and primary lateral veins, drying minutely granular, prominulous and alternating with secretory ducts. INFLORESCENCES erect, usually 2–3 (sometimes to 5) per axil; peduncle (4.5)5.6–18 cm long, terete, pale to medium green, faintly short-lineate to densely speckled; **spathe** 7–18.5 cm long (0.9–1.8 times longer than peduncle), moderately constricted above the tube; spathe blade pale green to white on both surfaces, acuminate at apex; spathe tube dark green, finely pale lineate, glossy outside, 4–8.5 cm long, 1.5–3 cm diam., reddish violet to maroon or magenta inside; **spadix** sessile; erect at anthesis, 7.6–13 cm long; pistillate portion 2.2–3.7(6.5) cm long, 1–1.4(2) cm diam. at middle, tapered slightly toward both ends; staminate portion clavate, 5.2–7.7 cm long; fertile staminate portion white, 8–10 mm diam. at base, 1–1.5 cm diam. at middle, 4–8 mm diam. ca. 1 cm from apex, broadest at the middle, abruptly tapered toward apex, weakly constricted just above the sterile portion; sterile staminate portion usually broader than the pistillate portion at anthesis, 8–15 mm diam., the lowermost flowers sometimes drying whitened; pistils 1.1–1.7(3.4) mm long, 7–9(17) mm diam.; ovary 4–6(10)-locular, 0.5–0.7(2.2) mm long, 0.7–0.9(1.7) mm diam., with sub-basal placentation; locules 0.5–0.7(2.1) mm long, 0.2–0.3(0.6) mm diam.; ovule sac 0.5–0.7 mm long; ovules 1 per locule, contained within sticky, transparent, gelatinous ovule sac, 0.2–0.3 mm long, as long as funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style 0.5–0.8(1) mm long, 0.6–0.7(1.7) mm diam., drying doughnut-shaped, similar to style type C; style funnel shallow with a small ring of stylar canals near the base; stigma subdiscoid, truncate, 0.4–0.5(0.8) mm diam., 0.1–0.3 mm high, covering almost entire style apex, with 1–5 depressions when dried, papillate, sessile, matte; the androecium truncate, prismatic, margins ± 4–5-sided, 0.6–1 mm long, 1.1–1.3 mm diam. at apex; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another and nearly contiguous to contiguous; pollen ± spheroidal, <0.1 mm long, <0.1 mm diam., scarce; sterile staminate flowers irregularly 4–6-sided, blunt, prismatic, 1–1.3 mm long, 0.9–1.2 mm wide. INFRUCTESCENCE with berries pale green (immature), greenish white to lavender.

Flowering in *Philodendron straminicaule* is believed to occur throughout much of the dry season to the mid-rainy season (January through August) in Panama, but flowering specimens have been seen from only April through August. Post-anthesis inflorescences have been seen from as early as March, and immature fruits as early as February, making it obvious that the plants have to be in flower as early as January. Post-anthesis inflorescences have also been collected from May through September and November, and immature fruits occur in March and July. The post-anthesis inflorescences from November suggest that flowering occurs as late as September or October.

Philodendron straminicaule is known only from the Cordillera de Guanacaste in northwest Costa Rica and in western Panama, from Chiriquí and Bocas del Toro to Coclé Province, at (710)950 to 2200 m elevation, generally in *Tropical Lower Montane rain forest* and *Premontane rain forest*, rarely in *Tropical wet forest.*

Philodendron straminicaule is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is characterized by its grayish (drying straw-colored), more or less brittle, glossy internodes, which are longer than broad; deciduous cataphylls; obtusely flattened, more or less spongy petioles; and triangular-ovate-cordate, green-drying blades with the lower surface drying densely and minutely granular and secretory ducts usually prominently visible and alternating with the minor veins. Also characteristic is the white spathe blade

and tube green outside and reddish violet to maroon inside.

Philodendron straminicaule is similar to *P. wilburii* var. *longipedunculatum*, but the latter species differs in having longer, more slender internodes; longer, unribbed to bluntly 1-ribbed cataphylls; typically smaller blades that dry brownish with mostly 3–4 primary lateral veins; and especially by having the peduncle usually as long as or even longer than the spathe (vs. usually less than length of spathe). It also differs in having orangish (rather than greenish white to lavender) berries.

The species may be confused with *P. alticola* and *P. smithii*. See those species for separation.

A noteworthy collection is *Croat 66503*, which has the veins on the lower leaf surface drying darker than the surface rather than paler, which is normally the case.

Collections from Costa Rica differ from those in Panama in having slightly smaller leaves with both the petioles and the blades shorter than those in Panama (petioles to 28 cm long and blades to 31 cm long in Costa Rica vs. petioles to 59 cm long and blades to 55 cm long in Panama). Nevertheless, the smaller leaves in Panama range down to only slightly larger than those in Costa Rica (with petioles as short as 32 cm long and blades to as small as 33 cm long).

One collection from Guanacaste (*Herrera 1473*) is unusual in having more narrowly triangular blades with concave margins, narrower posterior lobes, a parabolic sinus, and a D-type style. However, it is otherwise similar, having the same dried stem characteristics and 1 ovule per locule. More collections are needed to determine if this entity is distinct from *P. straminicaule*.

This species perhaps also occurs in Colombia based on collections from Valle Department (*Juncosa 2054*) at 580 m and from Gorgonilla Island, Cauca Department (*Killip & García 33060*). These collections differ from those in Panama in having blades with no obvious secretory ducts visible on the abaxial surface. In addition, the latter collection is from just 130 to 200 m elevation, substantially lower than where it is found in Panama.

Additional specimens examined. COSTA RICA. **Alejuela**: above Bijagua, slopes of Miravalles, *Gómez et al. 19171* (MO). **Guanacaste**: Parque Nacional Guanacaste, Estación Cacao, 1100 m, 10°55′45″N, 85°28′15″W, *Chávez 80* (INBIO, MO); Estación Mengo, 1100 m, 10°55′N, 85°28′W, *INBio 219* (CR, MO); Parque Nacional Rincón de la Vieja, SE slopes of Volcán Santa María, above Estación Hacienda Santa María, 900–1200 m, 10°47′N, 85°18′W, *Davidse et al. 23397* (CR, MEXU, MO, TEX); 1350–1400 m, 10°46′N, 85°49′W, *Herrera 1473* (CR, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, 21.4 km past Gualaca, 8°32′N, 82°19′W, *Hoover 1326* (MO); Continental Divide, 1200 m, 8°44′N, 82°17′W, *Croat 60350* (CM, MO); *60364* (AAU, CM, COL, CR, F, M, MO, PMA, UC, WIS), *60365* (K, MO, PMA, US); 8°45′N, 82°15′W, *McPherson 10867* (CR, MO, PMA); 2.8 mi. from Divide, 850–950 m, ca. 8°45′N, 82°15′W, *9675* (L, MO, PMA, US). **Bocas del Toro–Chiriquí**: Fortuna Dam area, Continental Divide, above Quebrada Arena, road to Oleoducto, 1150–1200 m, *Knapp & Vodicka 5658* (MO, PMA). **Chiriquí**: Cerro Colorado, above San Félix, 18–27 mi. off of Pan-American Highway, 1200–1500 m, *Croat 33146* (MO); 19.7 mi. N of Río San Félix, 1420 m, 8°31′N, 81°46′W, *Croat 74996* (MO); 33.1 km N of Río San Félix, ca. 1400 m, *Croat 37203* (MO, PMA); 20 mi. N of Río San Félix, 2000 m, *Croat 48446* (COL, K, MEXU, MO, PMA, VEN, W); 1420 m, *75010* (MO, PMA); vic. of Chame, 800–1200 m, *Croat 33440* (MO); 11.2 km from Chame, 1700 m, *Folsom 4889* (CAS, MO); 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69013* (B, CAS, CM, COL, CR, F, G, K, L, MEXU, MO, PMA, TEX, US); Cerro Horqueta, 7000 ft., *Blum & Dwyer 2591* (SCZ); Boquete, 5000–6000 ft., *Dwyer & Hayden 7736* (MO); 6500 ft., *von Hagen & Von Hagen 2073* (MO, NY); *2164* (MO, NY); Volcán Barú, along old road to Boquete, 1750–1900 m, 8°50′N, 82°30′W, *McPherson 11340* (K, MO); Cerro Pate Macho, ca. 5 mi. NE of Boquete, 1800–2200 m, *Croat 48562* (MO); 1900–2000 m, 8°46′N, 82°25′W, *66503* (MO); ca. 6 km NE of Boquete, 8°49′N, 82°23′W, *Grayum 6408* (CM, MO, PMA); 1600-1700 m, *Grayum et al. 6397* (MO, US); Río Palo Alto, 1300–1800 m, 8°47′N, 82°22′W, *Knapp et al. 2042* (MO); Fortuna Lake area, Gualaca–Chiriquí Grande, along Continental Divide, 1200 m, 8°44′N, 81°17′W, *Croat 74972* (MO, PMA); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60057* (AAU, B, CAS, F, K, L, MEXU, MO, PMA, SEL, U); ca. 4.6 mi. N of Los Planes de Hornito, *Stevens 18437* (MO); behind Vivero Forestal (now Centro de Científicos), 12 km N of Los Planes de Hornito, 1200–1300 m, 8°45′N, 82°12′W, *Knapp 4950* (MO); 10.1 mi. NW of Los Planes de Hornito, 1250 m, 82°17′W, 8°45′N, *Croat 49837* (BR, COL, MO, NY, TEX, UC), *50030* (MO, NY, TEX); vic. IRHE facilities, 1100–1200 m, 8°45′N, 81°18′W, *Croat 66542* (MO, PMA), *66584* (AAU, BR, CAS, CDBI, CM, DUKE, F, IBE, K, KYO, LE, MBM, MEXU, MO, NY, PE, PMA, RB, SCZ, UC, US); Río Chiriquí, 9.6 mi. beyond Los Planes de Hornito, 1300 m, *Croat 48733* (CR, MO); 11.8 mi. NW, 1400 m, *48686* (MO), *48703* (CM, MO), *48701* (CAS, MO); Quebrada Bonita, 1100 m, 8°45′N, 82°13′W, *Churchill 5262* (MO); Quebrada Ortega, 1200 m, 8°41′N, 82°14′W, *Churchill 5283* (MO); 8 mi. beyond Los Planes de Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67920* (AAU, CAS, MO, PMA, US). **Coclé**: El Copé region, Alto Calvario, ca. 6 km N of El Copé, 770 m, 8°38′N, 80°35′W, *Croat & Zhu 76761* (MO, PMA); 710–800 m, 8°39′N, 80°36′W, *Croat 68816* (MO); 900 m, *44576* (MO); 5.5 mi. N of El Copé, 850 m, 8°39′N, 80°36′W, *67574* (CM, MO, PMA, TEX). **Veraguas**: Santa Fe region, Escuela Agrícola Alto Piedra, ca. 5–8 km NE of school, 730–770 m, *Croat 25909* (MO, NY).

Philodendron strictum G. S. Bunting, Phytologia 60: 328. 1986. TYPE: Venezuela. Táchira: San Cristóbal–Chorro del Indio–Caño Seco–La Florida, km 20–22 (E of San Cristóbal), 1100–1125 m, 6 Mar. 1977, *Bunting & Borges 5001* (holotype, NY; isotypes, PT, VEN). Figures 393–395, 397, 398.

Terrestrial or hemiepiphytic; stems stout; internodes 3–4 cm long, 2.5–5 cm diam., usually broader than long, sometimes longer than broad, dark green to gray-green, semiglossy; roots moderately few, drying dark brown, semiglossy, sparsely scaly; cataphylls 25–40 cm long, unribbed to bluntly 1-ribbed, rarely bluntly 2-ribbed or sharply 1-ribbed, pale green, soft, turning yellowish and persisting semi-intact at upper nodes; **petioles** (47–56)63–105 cm long, subterete, obtusely D-shaped with faint medial rib, obtusely flattened adaxially, light green to gray-green, weakly glossy, sparsely dark lineate, drying usually light yellow-brown, sometimes blackened; sheath inconspicuous; **blades** ovate-cordate, conspicuously bicolorous, acuminate at apex (the acumen sometimes inrolled), cordate, sometimes sagittate at base, (24)38–66(74) cm long, (16)27–52 cm wide (1–1.3 times longer than wide), (0.5–1 times the petiole length), broadest near the middle; upper surface dark green, semiglossy, lower surface much paler, whitish, matte; anterior lobe (19–28)31–51(57–62) cm long, (19)27–48(53–56) cm wide, (1.7–2.8(3.3) times longer than posterior lobes); posterior lobes 12–23 cm long, 8.6–26 cm wide, obtuse to broadly rounded; sinus usually spathulate, sometimes hippocrepiform; midrib flat, paler than surface above, convex and darker below; basal veins 7–10 per side, with 0–2 free to base, part of the remainder coalesced 1–12.4 cm; posterior rib sometimes not naked, often obscurely naked for 1.5 cm, rarely 3.5 cm; primary lateral veins 5–11 per side, departing midrib at a 50–65° angle, deeply sunken above, convex and darker below, usually prominently downturned before meeting midrib; minor veins numerous, fine, indistinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect-spreading, 1–4 or more per axil; peduncle (6)11–15 cm long, 1–1.5 cm diam., with thin, yellowish epidermis; **spathe** 13–17.7 cm long, 2.5–4.3 cm diam. (0.9–2.3 times longer than peduncle), moderately constricted above the tube (very slick inside), 2.7 cm diam. at constriction; spathe blade light green to whitish, tinged purple-violet (B & K red-purple 3/2.5), sparsely short-white-lineate medially outside, margins paler, (opening elliptic in face view, 10.7 cm long, 4.8 cm wide), light green to whitish and suffused red inside, drying dark to reddish brown; spathe tube green to purple-violet (B & K red-purple 3/2.5) outside, 4 cm diam., maroon or violet-purple inside; **spadix** sessile; bluntly pointed at apex, 9.2–16 cm long; pistillate portion weakly tapered toward apex, 2.1–3.9 cm long in front, (1.6)3–3.3 cm long in back, 0.6–1.4 cm diam. at apex, 1–1.5 cm diam. at middle, 1.3–1.5 cm wide at base; staminate portion 8.9–11.9 cm long; fertile staminate portion somewhat ellipsoid, sometimes ovate to tapered, 1.1 cm diam. at base, 1.2–1.3 cm diam. at middle, 8–9 mm diam. ca. 1 cm from apex, broadest in the middle or sometimes just above the base, narrower than the pistillate portion, as broad as the sterile portion; sterile staminate portion narrower than the pistillate portion, 1–1.4 cm diam.; pistils (1.1)2.7–3.4(5.4) mm long, 1.3–1.6 mm diam.; ovary (4)5–6-locular, 1.8 mm long, 1.3–1.7 mm diam., with axile placentation; locules 1.8 mm long, 0.6 mm diam.; ovules 20–28 per locule, 2-seriate, 0.2–0.4 mm long, longer than funicle; funicle 0.1 mm long, adnate to lower part of partition, style 0.7–0.9 mm long, 1.3–1.6 mm diam., similar to style type B; style apex flat; stigma subdiscoid, truncate, 1.1–1.3 mm diam., 0.3–0.5 mm high, covering entire style apex; the androecium prismatic, truncate, oblong, irregularly 4–6-sided at apex 0.9 mm long, 1.6–2 mm diam. at apex; thecae oblong, ± parallel to one another, nearly contiguous; sterile staminate flowers blunt, prismatic, irregularly 4–6-sided, 1.8–2.9 mm long, 0.9–2.4 mm wide. INFRUCTESCENCE 2 cm wide; seeds pale yellowish, 0.9 mm long, 0.3 mm diam.

Flowering in *Philodendron strictum* apparently occurs throughout the dry season and first half of the rainy season in Central America (January through September, though no flowers were seen in May). South American flowering collections have been seen from February and July, and post-anthesis inflorescences (or immature fruits) from January through November. Mature fruits have been seen only from September.

Philodendron strictum ranges from Costa Rica to western Panama, Venezuela (Táchira), Colombia (Antioquia, Chocó), and Ecuador (Carchi, Esmeraldas). In Costa Rica, this species occurs at 850 to 1525 m, and in Panama at 680 to 1665 m elevation in *Lower Montane rain*, *Premontane rain*, and *Tropical wet forest* life zones. In Colombia, this species has been collected at 100 to 150 m in Chocó and Valle Departments, and in Antioquia at 1560 m. In Venezuela, it is known only from the state of Táchira in the southwestern part of the country, at 1000 to 1250 m elevation in *Premontane wet forest.* It was reported erroneously (owing to a typographical error) by Croat and Lambert (1986) from 110 to 1330 m.

Philodendron strictum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Impolita.* This species is characterized by its usually terrestrial habit; thick stems; short internodes; thick, yel-

lowish, unribbed to bluntly one-ribbed cataphylls persisting semi-intact at the upper nodes; obtusely flattened to D-shaped petioles usually drying pale yellow-brown; and ovate-cordate blades with the lower surface whitish and matte.

Philodendron strictum is most easily confused with *P. hebetatum*, which shares blades with whitish, matte lower surfaces, as well as yellow-drying cataphylls and petioles. Both species are easily identified by these features alone. The two species are sympatric in at least one area along the Fortuna Dam road in Panama but remain distinct by virtue of their respective habits and blade shapes. *Philodendron hebetatum* differs in being consistently an appressed epiphyte and in having a triangular-ovate blade vs. a generally terrestrial habit and consistently ovate blades for *P. strictum*. Juvenile plants of the two species, at this stage both terrestrial, are quite distinct with the blades of *P. hebetatum* more elongate (2.5–3 times longer than broad), while those of *P. strictum* are more broadly ovate (1.2–2.5 times longer than wide).

This species is also easily confused with the often syntypic *P. thalassicum*, which differs in having blackened rather than pale yellow-brown petioles, cataphylls promptly weathering to pale fibers vs. usually persisting yellowish and semi-intact in *P. strictum* and internally greenish to white spathes (vs. maroon or violet-purple in *P. strictum*). In addition (at least in Panama), the petioles of *P. thalassicum* are more sharply D-shaped vs. obtusely flattened in *P. strictum*.

A collection from 1875 m elevation in Antioquia Department, Colombia (*McPherson 12939*), possibly belongs to this species but differs in having reddish brown cataphylls that are more fragmented on drying. It also has the petioles drying dark brown, not yellowish as is typical for the species in Colombia and Ecuador.

Additional specimens examined. COSTA RICA. **Alajuela**: San Ramón, Bajo Rodríguez, 1025–1100 m, *Croat 78888* (CR, INB, MO). **Cartago**: ca. 11 mi. NE of Turrialba, 850 m, *Croat 43354* (MO); Turrialba–Limón, Hwy. 32, ca. 11 mi. S of Siquirres, 650 m, *Croat 43335* (MO); 31 km S of Siquirres on road to Turrialba (CR-10), 850 m, 9°57′N, 83°36′W, *Thompson & Rawlins 1167* (CM); Shipirí, Moravia de Chirripó, 900–1000 m, *I. Chacón 9* (MO); Tapantí, *Nilsson & Chacon 236* (CR); *Croat 79039* (MO). **Puntarenas**: ca. 1 km S of San Vito, 1100 m, *Croat 66168* (CR, G, MO, NY, PMA); Las Cruces, near San Vito de Java, ca. 4000 ft., *Croat 32959* (MO); N of Palmar Norte, trail to Jalisco, 50–700 m, *Croat 35208* (MO). **San José**: San Isidro de El General–Dominical, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35250* (MO); 990–1100 m, *Croat & Hannon 79105* (CR, INB, MO); Braulio Carrillo National Park, 1400 m, *Croat 78811* (CR, INB, MO); Tarrazu, vic. Hormiguero, 1100-1200 m, *Croat 78939* (CR, INB, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Continental Divide, 1170 m, 8°44′N, 82°17′W, *Croat 66649* (AAU, B, CAS, CM, COL, CR, F, G, K, L, MEXU, MO, NY, PMA, US, VEN); 1000 m, 8°48′N, 82°12′W, *Churchill et al. 4646* (MO); ca. 1200 m, 8°44′N, 82°17′W, *Croat & Grayum 60326* (B, CM, K, MO, RSA, US); 2.2 mi. N of Continental Divide, 820 m, 8°45′N, 82°16′W, *Croat 60401* (MO); 825 m, 8°45′N, 82°15′W, *McPherson 7361* (B, K, MO, PMA, RSA); 1.2 mi. N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat 60475* (MO, PMA). **Chiriquí**: Cerro Colorado, 9–10 mi. road to Chame, 1200–1500 m, *Croat 33272* (MO); 7.7 mi. beyond Chame, 1420 m, 8°31′N, 81°46′W, *74995* (MO); Chame, 1600 m, *Kress et al. 86-1925* (SEL); 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69064* (MO); 6.5 km beyond Chame, 1660 m, 8°30′N, 81°46′W, *Croat 74991* (MO); Fortuna Dam area, Gualaca–Chiriquí, 1200 m, 8°46′N, 82°16′W, *Croat 68030* (F, MO); E of main camp at dam site, 1400–1500 m, *Folsom et al. 5448* (MO); trail to Río Hornito weather station, 1100–1200 m, 8°45′N, 82°15′W, *Thompson 5041* (CM); 8°45′N, 82°18′W, *Croat & Zhu 76311* (AAU, CM, COL, CR, DUKE, EAP, GH, IBE, MEXU, MO, P, QCNE, RSA, US); *76375* (CAS, CM, COL, CR, DUKE, ENCB, F, GB, K, L, MEXU, MO, NY, P, SEL, WIS); Continental Divide, 1200 m, 8°44′N, 81°17′W, *Croat 74971* (MO, PMA); Quebrada Arena, just S of Continental Divide, 1050 m, 8°45′N, 82°16′W, *Hammel et al. 14707* (MO); Quebrada Los Chorros–Quebrada Honda, to N of reservoir, 8°45′N, 82°14′W, *H. Churchill & A. Churchill 6166* (MO, NY); vic. IRHE facilities at dam, 1200–1300 m, 8°45′N, 82°18′W, *Croat 66543* (AAU, DUKE, F, M, MEXU, MO, PMA); Gualaca–Chiriquí Grande, 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *Croat 67840* (CM, MO, PMA); 8.4 mi. beyond Los Planes de Hornito, 1130 m, 8°44′N, 82°14′35″W, *67870* (G, M, MO). **Coclé**: El Copé region, Alto Calvario, ca. 6 km N of El Copé, 8°39′N, 80°36′W, *Croat 68818* (MO); 680–770 m, 8°39′N, 80°36′W, *74852* (MO, W); 700 m, 8°38′N, 80°35′W, *Croat & Zhu 76796* (MO, NY); El Valle region, vic. of La Mesa, N of El Valle de Antón, Cerro Gaital, 900–1000 m, 8°37′N, 80°08′W, *Croat 67227* (B, CAS, CM, K, MO). **Veraguas**: Santa Fe region, Alto de Piedra, 800–950 m, 8°33′N, 81°08′W, *Croat 67003* (CAS, MO); Parque Nacional Cerro Tute, 0.5 mi. N of Alto Piedra, 800–1030 m, *Croat & Zhu 76885* (MO); 1000–1250 m, *Croat 48920* (MO).

Philodendron subincisum Schott, Oesterr. Bot. Z. 9: 99. 1859. TYPE: Mexico. Veracruz: Papantla, 20°27′N, 97°19′W, *Karwinski s.n.* (holotype, LE? destroyed?); Schott ic. 2636 (neotype, here designated, W). Figures 396, 401, 402.

Hemiepiphytic; leaf scars conspicuous, 1–1.5 cm long, 1–2 cm wide; internodes 1.2–6 cm long, 2.7–3 cm diam., broader than long, tan to reddish brown, epidermis with loose flakes; roots few to numerous per node; cataphylls moderately spongy, 23–34 cm long, unribbed, drying sharply 1-ribbed in lower one-third, pale green, drying tan to reddish brown, persisting semi-intact, eventually fibrous; **petioles** 55.5–68 cm long, 1.4–1.5 cm diam., terete, medium green, drying yellowish tan to reddish

tan, surface dark green diffuse-lineate; **blades** narrowly ovate, coriaceous, semiglossy, moderately bicolorous, long acuminate at apex, sagittate at base, (40)57.5–72 cm long, (24)32.5–37 cm wide (1.7–1.8 times longer than wide), (ca. 1 time longer than petiole), margins hyaline, markedly sinuate, upper surface drying brown, lower surface drying yellow-red to brown; anterior lobe (32.5)40–49 cm long, (10)17.6–18 cm wide (2.3–3.3 times longer than posterior lobes); posterior lobes (10)17–18 cm long, 16–16.5 cm wide, obtuse; sinus hippocrepiform or closed and obovate with lobes overlapping, acute when young; midrib broad, flat, paler than surface above, convex, concolorous below; basal veins 4–9 per side, first (second) pair free to base, most coalesced 1–4 cm, 2–3 coalesced to 5.5 cm; posterior rib not naked or obscurely naked for ca. 1 cm; primary lateral veins 5–7 per side, departing midrib at a 50–60° angle, sunken, paler than surface above, convex, concolorous below; minor veins flat, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES 2 per axil, ± erect; peduncle 7.5–10 cm long, 1.3 cm diam., medium green; **spathe** 16.5–20 cm long, 3.5 cm diam. (closed), 5 cm diam. (opened), constricted above the tube, acuminate at apex, margins paler; spathe blade semiglossy, greenish outside, white inside; spathe tube more ellipsoid, maroon-purple outside, bright cherry-red inside; **spadix** not seen.

The flowering phenology of *Philodendron subincisum* is unknown. The only modern collection (*Moore & Bunting 8952*) is sterile.

Philodendron subincisum is endemic to Mexico, known only from northern Veracruz in the Poza Rica region, at less than 500 m elevation in "Selva Mediana Subperennifolia."

Philodendron subincisum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium.* This species is characterized by its large, thick stems, short internodes, deciduous cataphylls, subterete petioles, ovate-cordate blades with markedly sinuate margins, two short-pedunculate inflorescences per axil, spathe tube maroon-purple outside and bright cherry-red inside, and spathe blade green outside and white within.

Philodendron subincisum is apparently rare, having been collected only once (*Moore & Bunting 8952*) since the type gathering.

Philodendron subincisum appears to be most closely related to *P. sagittifolium* based on most features, but it may represent a hybrid. Bunting (1965) even suggested that *P. radiatum* was closely allied to *P. subincisum.* Judging from its rarity, the latter taxon might be a hybrid between *P. radiatum* and *P. sagittifolium.* Because of its ovate blade with sinuate margins, it is not confused with either of the above species. Perhaps most easily confused with *P. subincisum* is *P. radiatum* var. *pseudoradiatum.* That taxon differs in occurring only on the Pacific slope and in having ovate-triangular blades with proportionately narrower and longer lobes.

The inflorescence of this species remains poorly known. Collected in sterile condition by Moore and Bunting (*8956*), the species later flowered in cultivation at Cornell University. The flowering specimen was apparently vouchered by Bunting, but the whereabouts of the collection are unknown. Much of the information concerning the species is based on photographs published by Bunting (1965).

Additional specimen examined. MEXICO. **Veracruz**: Rancho El Huasteco, 14.6 mi. from Tuxpan on road to Tihuatlán, *Moore & Bunting 8956* (BH, MO).

Philodendron sulcicaule Croat & Grayum, sp. nov. TYPE: Costa Rica. Limón: 7 km SW of Bribrí, 100–250 m, ca. 9°36′N, 82°54′W, 4 May 1983, *Gómez, Liesner & Judziewicz 20473* (holotype, MO–3160203; isotypes, B, CR, K, PMA, US). Figures 399, 400, 403.

Planta hemiepiphytica; internodia 6–16 cm longa, 5–13 mm diam., profunde sulcata; cataphylla 12 cm longa, incostata, vel acute 1-costata, raro acute 2-costata, decidua intacta; petiolus 11–20 cm longus, subteres, leniter complanatus adaxialiter; lamina ovato-cordata, abrupte vel longa acuminata, 14.5–24 cm longa, 9.6–15 cm lata; nervis basalibus 3 utroque, infirmis; nervis lateralibus I obscuris; inflorescentia 1–4(5); pedunculus tenuis, 3.5–10 cm longus, 1–3 mm diam.; spatha (4.5)5.8–11 cm longa, omnino alba, tubo spathae intus rubro, roseo aut purpureo basi; pistilla 4–5-locularia; loculi 1-ovulati.

Hemiepiphytic vine; stem scandent, drying yellow, glossy; internodes deeply sulcate, prominently ribbed, semiglossy, 6–16 cm long, 5–13 mm diam., longer than broad, olive-green; epidermis becoming brown, breaking free on bending stem; roots red-brown, slender, curled, 8–20 cm long; cataphylls 12 cm long, unribbed to sharply 1-ribbed, rarely sharply 2-ribbed, green rarely pink, deciduous intact; **petioles** 11–20 cm long, 4–8 mm diam., subterete, dark green, weakly flattened adaxially, semiglossy; **blades** ovate-cordate, subcoriaceous, semiglossy, moderately bicolorous, abruptly- to long-acuminate at apex (the acumen apiculate, to 4 mm long), cordate at base, 14.5–24 cm long, 9.6–15 cm wide (1.3–1.9 times longer than wide), (0.9–1.6 times longer than petiole), about two-thirds as long as petiole, margins drying moderately undulate, upper surface dark green, drying usually

dark brown, semiglossy to matte, lower surface paler, drying light brown to greenish brown, sometimes yellowish brown, semiglossy; anterior lobe 10–19.6 cm long, 7–15 cm wide (2.6–3.8 times longer than posterior lobes); posterior lobes 3.5–6 cm long, 2.7–6.4 cm wide, rounded-obtuse to nearly acute; sinus arcuate with blade decurrent on petiole to short-hippocrepiform; midrib flat to weakly raised, concolorous above, convex, concolorous to paler than surface below; basal veins to 3 per side, weak, 1 sometimes free to base, the remainder coalesced 0.5–2 cm; posterior rib naked for all its length; primary lateral veins obscure above, obscure below; minor veins distinct, fine, close, arising from the midrib only; "cross-veins" sometimes visible. INFLORESCENCES 1–4(5) per axil; peduncle 3.5–10 cm long, 1–3 mm diam., reddish, whitish or purplish, slender; **spathe** (4.5)5.8–11 cm long, (0.9–1.1(2) times longer than peduncle), weakly constricted midway, 5 mm diam. at constriction, white throughout, becoming greenish (post-anthesis), rarely reddish (*Gómez et al. 20473*), cuspidate-acuminate at apex (the acumen ca. 1.5 mm long), white inside; resin canals appearing as intermittent lines in lower two-thirds of spathe, extending into upper part of spathe tube, drying blackened; spathe tube 3–4 cm long, red, pink, or purple at base inside; **spadix** sessile; slender, acute at apex, 4.5–7.7 cm long, broadest at the middle of the staminate portion, constricted scarcely or not at all above the sterile staminate portion; pistillate portion white, 2.5 cm long, 4.5 mm diam. midway, 3.5–4.5 mm diam. at apex and at base; staminate portion 3–5.2 cm long; sterile staminate portion cream, 3–4 mm diam.; pistils white; ovary 4–5-locular, with ± subbasal placentation; locules 0.4 mm long, 0.2–0.3 mm diam.; ovule sac 0.4 mm long; ovules 1 per locule, contained within translucent or transparent ovule sac, 0.2–0.3 mm long; funicle 0.1–0.2 mm long (can be pulled free to base), style similar to style type B; style apex flat; stigma subdiscoid, unlobed, ± truncate, 0.4–0.5 mm diam., 0.1 mm high, covering center of style apex; the androecium margins irregularly 4–6-sided, 0.6–1.2 mm long. INFRUCTESCENCE peduncle, 8 cm long, 1 cm diam.

Flowering in *Philodendron sulcicaule* occurs during the dry season and early wet season (December through May, though no flowering collections have been seen from April). Post-anthesis collections have been seen from March and April. No fruits have been seen.

Philodendron sulcicaule ranges from extreme southeastern Costa Rica to the Atlantic slope of Panama, from 100 to about 700 m elevation (though generally less than 300 m) in *Premontane wet forest* transition to *Tropical wet forest* life zones.

Philodendron sulcicaule is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* The species is characterized by its scandent habit; deeply sulcate stems drying yellow and glossy; unribbed, deciduous cataphylls; subterete petioles weakly flattened adaxially; and ovate-cordate blades with obscure primary lateral veins and up to four pairs of weak basal veins. Also characteristic are the numerous (up to five per axil), small, slenderly pedunculate inflorescences with spathes white outside (sometimes tinged red) and red to purplish in the base of the tube.

Philodendron sulcicaule appears closest to an undescribed species from Bajo Calima, Valle Department, Colombia (e.g., *Croat 70137*). Though the latter species has the same habit, petiole shape, leaf size and shape, and ribbed yellowish stems, it differs in having white cataphylls, usually 3–4 primary lateral leaf veins, and 3–5 basal veins with a well-developed posterior rib. In addition, the spathe tube is reddish outside and the entire inner surface is creamy-white (vs. usually white outside and reddish to purplish inside the tube in *P. sulcicaule*).

In Central America, *Philodendron sulcicaule* resembles *P. purpureoviride* and *P. microstictum,* both of which are vines with similar leaves. *Philodendron purpureoviride* differs in having solitary, stout inflorescences (instead with up to three or four smaller inflorescences) and leaf blades with distinct primary lateral veins. *Philodendron microstictum* differs in having blades broader than long (vs. longer than broad in *P. sulcicaule*).

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 3.2 mi. N of Continental Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60249* (MO). **Coclé**: Bismarck, 2000–3000 ft., *Williams 628* (NY); 16.7 km N of turnoff to Coclesito from Llano Grande, 700 ft., *Hammel 1791* (MO). **Colón**: Santa Rita Ridge Road, ca. 22 km from Transistmian Highway, 500 m, 9°25′N, 79°40′W, *Hammel et al. 14504* (B, CAS, K, MO, PMA, US); E Santa Rita Ridge, *Correa 670* (MO, PMA); Río Iguanita, ca. 1 mi. upstream, *Kennedy & Dressler 3481* (F); Sabanitas–Portobello, Río Piedras Lumber Road, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75167* (CM, MO, PMA, US); Río Guanche, 30–100 m, *Croat 79344* (PMA, MO). **Panamá**: El Llano–Cartí, 12–16 km N of Pan-American Highway, 150–400 m, *Kennedy et al. 3162* (MO); Mile 10, 330 m, *Croat 33734* (CM, F, MO); Mile 12, 200–500 m, *Liesner 1154* (MO, US); ca. 4.6 mi. N, ca. 350 m, 9°15′N, 79°W, *McPherson & Merello 8163* (B, F, MO); Mile 4, 500 m, *Croat 49140* (MO). **San Blas**: El Llano–Cartí road, Mile 12, ca. 1000 ft., *Antonio 3781* (MO); Mile 14, 300 m, 9°15′N, 79°W, *Croat 69246* (CAS, CM, CR, L, MO, NY); Mile 9, 350 m, 9°20′N,

79°W, *Croat & Zhu 76565* (MO). **San Blas–Panamá**: Kuna Divide trail, W of El Llano–Cartí Road, 250 m, 9°20′N, 79°W, *McPherson 11868* (MO); Cordillera de San Blas, Pacific slope headwaters of Río Piria, 200–400 m, 9°12′N, 78°16′W, *H. Herrera et al. 1143* (K, MO, PMA, US).

Philodendron tenue K. Koch & Augustin, in A. Braun et al., Append. gen. sp. Hort. berol. 1854: 7. 1854–1855. TYPE: Cultivated at Berlin, origin unknown (holotype, B? lost); Schott ic. 2465 and 2466 (neotype, here designated, W). Figures 404–407, 413, 414.

Philodendron gracile Schott, Prod. syst. Aroid. 244. 1860. TYPE: Costa Rica. *Wendland s.n.*, not seen (holotype, W? now lost; impression of type is at K); Schott ic. 2687–2688 (neotype, here designated).

Philodendron ecuadorense Engl., Bot. Jahrb. Syst. 26: 531. 1899. TYPE: Ecuador. Manabí, *Eggers 15221* (holotype, B; isotype, F).

Philodendron sodiroanum Engl., Bot. Jahrb. Syst. 26: 531. 1899. TYPE: Ecuador. Pichincha: Nanegal, *Sodiro 47* (holotype, B).

Usually hemiepiphytic, rarely terrestrial or epilithic; stem usually appressed-climbing, thick, short, leaf scars inconspicuous; internodes striate, 2–3.5 cm long, 1–2.5 cm diam., about as long as broad, dark green to olive-green; roots drying tan to brownish red to blackish, smooth, elongate, 7–28 cm long, 0.2–0.5 cm diam., usually few per node, rarely numerous per node, dense, spreading at the nodes, epidermis peeling; cataphylls membranous, 28–31 cm long, 8 cm broad at base, usually unribbed, sometimes bluntly or sharply 1-ribbed to sharply 2-ribbed, green, red or purplish green, pale white-striate, drying brownish to reddish brown, persisting intact, eventually fibrous. LEAVES ± erect; **petioles** 29–107 cm long, 2–11 mm diam., erect, ± terete, stiff, firm, dark green, sometimes somewhat flattened with a low medial rib adaxially, surface weakly semiglossy, weakly light green striate with many small, fine ridges; geniculum thicker than petiole, 3–4 cm long, scurfy, slightly paler than petiole; **blades** ovate to ovate-triangular with prominent posterior lobes, chartaceous to subcoriaceous, moderately bicolorous, narrowly acuminate, sometimes long-acuminate at apex (the acumen inrolled, 1–4 mm long), cordate at base, 31–78 cm long, 16–52 cm wide (1.2–3.1 times longer than wide), (0.6–1.4 times longer than petiole), margins weakly undulate, upper surface gray-green to dark green, glossy, lower surface semiglossy, paler; anterior lobe 30.5–60 cm long, 14–34 cm wide (1.5–3.8 times longer than posterior lobes), broadest at point of petiole attachment; posterior lobes 10–29.5 cm long, 6–16.5 cm wide, broadest at or near the middle, directed downward and outward, sometimes inward, obtuse to subrounded to bluntly acute; sinus triangular, acute to almost obtuse, sometimes closed, 4.5–17 cm deep; midrib flat to sunken, concolorous to slightly paler than surface above, raised, concolorous, drying somewhat paler than surface below; basal veins 5–7 per side, with 0(1) free to base, part of the remainder coalesced 2–10.5 cm; posterior rib not naked; primary lateral veins (6)8–14(20) per side, departing midrib at a 65–90° angle, ± straight or weakly arcuate to the margins, prominently to narrowly sunken above, raised to convex below; interprimary veins as conspicuous as primary lateral veins, weakly sunken and concolorous above, weakly raised and concolorous below; minor veins moderately visible to distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, to 4 per axil; peduncle 2–11 cm long, 3–18 mm diam., pale green, drying reddish brown, heavily white-lineate, drying longitudinally fissured; **spathe** erect to erect-spreading, coriaceous, acuminate at apex, 7–14 cm long, (1.3–4.4 times longer than peduncle), moderately constricted above the tube, 2.1 cm diam. at constriction, short-lineate throughout; spathe blade weakly lanceolate, greenish white, sometimes heavily tinged red outside, 4–8 cm long, 2.1 cm diam., (opening 3.6 cm long), white to pale green inside; spathe tube ovoid, medium to dark green, usually tinged red or sometimes dark violet outside, white-striate with clear margins in front, short, pale green lineate in back outside, 3–7 cm long, 2–3.5 cm diam., white to pale green, sometimes red at base inside, sometimes sparsely white-spotted; **spadix** sessile; 6–12 cm long; pistillate portion yellowish green to pale green, weakly tapered upward, 2.8–4 cm long in front, 1.9–2.2 cm long in back, 1.1–1.6 cm diam. at middle, 1.75 cm wide at base, 0.9–1.5 cm ca. 1 cm from apex, with 12–14 flowers per spiral; staminate portion 5.3–7.1 cm long; fertile staminate portion white, drying orange reddish to light reddish, 1–1.1 cm diam. at base, 1.2–1.5 cm diam. at middle, 7–10 mm diam. ca. 1 cm from apex, broadest in the middle, as broad as to slightly broader than the pistillate portion, as broad as to narrower than the sterile portion, 27–35 flowers visible per spiral; sterile staminate portion as broad as to broader than the pistillate portion, pale brown, 11–17 mm diam.; pistils 2.7–3.1(6.2) mm long, 1.2–1.7(3.9) mm diam.; ovary 4–5-locular, 1.6–2(5.9) mm long, 1.2–1.7(3.9) mm diam., with axile placentation; locules 1.6–2(4.2–5.9) mm long, 0.4–0.7(1.1) mm diam.; ovules 12–14 per locule, 2-seriate, 0.4 mm long, longer than funicle; funicle 0.2(0.5) mm long, adnate to lower part of partition,

style 0.5–0.6 mm long, 1.2–1.7 mm diam., similar to style type B; style apex flat; stigma cupullate, ± hemispheroid, 1.1 mm diam., 0.4–0.6 mm high, covering center of or entire style apex, depressed medially with 6–8 holes; the androecium truncate, prismatic, margins irregularly 4–6-sided, (0.3)0.7–0.9 mm long, 1.1–1.4 mm diam. at apex; thecae oblong, 0.3–0.4 mm wide, ± parallel to one another, nearly contiguous; sterile staminate flowers irregularly 4–6-sided, mostly prismatic, sometimes clavate, blunt, 1.3–2.5 mm long, 1.4–2.5 mm wide. INFRUCTESCENCE with fruits purplish.

Flowering in *Philodendron tenue* occurs during the dry season and early rainy season (January through August, perhaps especially April and May). Post-anthesis collections are from January to October, and immature fruits are known from April through November.

Philodendron tenue ranges from Nicaragua to southern Ecuador (El Oro) on the Pacific slope, and in Venezuela along the foothills of the Sierra de Perijá (Zulia), through the Cordillera de la Costa (Yaracuy to the Distrito Federal at Cerro Naiguatá) and in the foothills of the Cordillera de Mérida south to Apure. In Central America it ranges from 20 to 1400 m in elevation in *Premontane wet forest*, rarely in *Tropical moist forest*. In Colombia it has been collected to 2300 m, and in Ecuador to 1930 m. *Philodendron tenue* is ecologically quite versatile in South America, where it occurs in *Tropical thorn woodland, Premontane thorn woodland, Tropical dry forest, Tropical moist forest,* and *Premontane wet forest* life zones.

Philodendron tenue is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa*. This species is characterized by its epiphytic habit, short internodes, persistent cataphyll fibers, more or less terete petioles (equal to or longer than the blades), and especially by its ovate to ovate-triangular blades with prominent posterior lobes often directed outward, narrow to almost closed V-shaped sinus with the posterior ribs not at all naked, and anterior lobe with numerous close primary lateral veins.

Philodendron tenue is similar and perhaps related to *P. maguirei* G. S. Bunting, but that species is terrestrial, has fewer primary lateral veins (typically 3–6 vs. 8–20 for *P. tenue*), and petioles drying straw-yellow (vs. green to brown for *P. tenue*).

The species can be confused with narrow-leaved epiphytic forms of *P. thalassicum* in Costa Rica, but that species has a somewhat glaucous epidermis on the abaxial blade surface and also uniformly greenish spathes.

It is strange that *P. tenue* is found on both sides of the Andes (an unusual pattern except for the most weedy of species), but still does not extend southward from Venezuela. It should certainly be expected at least in Amazonian Colombia.

Additional specimens examined. COSTA RICA. **Alajuela**: Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36000* (MO); *36294* (MO); 13.8 km N of Bijagua, 100–150 m, *36450* (MO); 8.5 km NE of Villa Quesada, ca. 600 m, *Croat 46969* (MO); 7.5 km N of Río Balsa, 700–800 m, ca. 10°10–15′N, 84°30–35′W, *Stevens 13861* (MO); 17 km NW of San Ramón, 785 m, 10°14.15′N, 84°33′W, *Croat 68161* (CR, F, M, MO); 3.5–4 mi. W of center of San Ramón, 800 m, *46778* (MO); Río San Rafael, W of La Marina, 500 m, 10°23′N, 84°23′W, *Burger & Stolze 5003* (CR, F, GH, NY, US); *5013* (CR, GH, US); San Carlos–San Pedro, ca. 150 m, *Horich s.n.* (M). **Cartago**: Río Gato, 12 km S of Turrialba by air, 4 km SE of Pejibaye, 700 m, 9°48′N, 83°42′W, *Liesner 14360* (CR, MO); Río Reventazón valley, 3 km SE of Turrialba, 500–600 m, *Holm & Iltis 190* (A, BM, G, GH, U); 525–600 m, 9°54′N, 83°39′W, *Liesner et al. 15340* (CR, MO, WIS); Cartago, 4250 ft., *J. D. Smith 5964* (US). **Guanacaste**: Lake Arenal, 550–850 m, 10°27′N, 84°50′W, *Hammel et al. 15140* (MO); Continental Divide, La Chirripa Ridge, 4 km NE El Dos de Tilarán, 1000 m, 10°25′N, 84°53′W, *Haber et al. 4859* (MO); Río Chiquito, Tilarán–Arenal, Zona Monteverde, 700 m, 10°23′N, 84°51′W, *Haber & Bello 8241* (CR, MO); Río Aguas Verdes, 600 m, *Rivera & Dennis 1050* (CR, INB, MO); Río Negro, 1100 m, *Rivera 718* (CR, INB, MO). **Heredia**: vic. Porto Viejo, near Río Sucio, 20 m, *Croat 35691* (F, MO); Río Peje–Río Sardinalito, Volcán Barva, 700–950 m, 10°17′30″N, 84°04′30″W, *Grayum 6924* (MO); *6886* (CR, MO); La Selva Field Station, ca. 100 m, *Grayum 2626* (DUKE); *2901* (DUKE); Parque Nacional Braulio Carillo, above Río Sucio, 5–600 m, *Pennington et al. 11536* (K). **Limón**: Guápiles, 300–500 m, *Standley 37415* (US); *37451* (US); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8366A* (RSA); *8742* (MO, RSA); W of Guápiles, Quebrada Danta, 360 m, 10°12′N, 83°49′W, *Croat 68427* (MO); Finca Castilla, 30 m, *Dodge & Goerger 9270* (MO); Cerro Coronel, 20–170 m, 10°41′N, 83°38′W, *Stevens 23637* (CR, MO); *24462* (CR, MO); Pococi, Sardinas, 15–20 m, *Araya 510* (CR, INB). **Puntarenas**: Osa Peninsula, 500 m, *G. Herrera 4013* (CR, INB, MO); Chacarita–Rincón de Osa, 10 km W of Chacarita, ca. 100 m, 8°45′N, 83°18′W, *Croat & Grayum 59893* (CR, MO); Piedras Blancas, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67698* (CAS, CR, MO); vic. Golfito, 100 m, 8°40′20″N, 83°12′10″W, *Hammel 18399* (CR, MO); 6 km S of San Vito de Java, 3500 ft., *Raven 21882* (BM, CR, DS, F); 4000 ft., *22009* (CR, DS, F, WIS). **San José**: Without locality, *Yeilding 235* (CR, F). HONDURAS. **Gracias a Díos**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9293* (MO, TEFH, UNAH). **Olancho**: Poncaya, *Blackmore & Heath 1994* (BM); Río Olancho, 19 mi. NE of San Esteban, 550 m, 15°29′N, 85°43′W, *Croat & Hannon 64475* (B, MO). NICARAGUA. **Boaco**: Cerro Mombachito, 700–1000 m, *Grijalva & Araquistain 80* (MO). **Chontales**: La Libertad, 500–700 m, *Standley 9056* (F); 4 km NW of Santo Domingo, 280 m, ca. 85°06′W,

12°17′N, *Grijalva 3806* (MO). **Jinotega**: La Salvadora–La Palestina, Hwy. 3, 1100–1150 m, ca. 13°04–05′N, 85°53–54′W, *Stevens & Grijalva 15369* (MO); Río Bocay, Salto Kayaska, 190–340 m, ca. 13°51′N, 85°22′W, *Stevens et al. 16464* (CAS, MO); Caño Litutus, ca. 175 m, ca. 13°58′N, 85°21′W, *Stevens et al. 16665* (MO). **Matagalpa**: NW of Cerro Musún, trail to Paiwás, 800–1200 m, *Araquistain & Moreno 2535* (MO); 300–600 m, *2470* (MO); trail to Paylo, 500–800 m, *2568* (K, MO); Macizos de Peñas Blancas, 1000–1400 m, ca. 13°14–15′N, 85°38–39′W, *Stevens et al. 21074* (MO); Cerro Musún, Río Bilampí, 500–800 m, 13°N, 85°14′W, *Araquistain & Moreno 2351* (MO); NW of Cerro Musún, 4 km SW of Wanawás, 200–500 m, 13°00–01′N, 85°14′W, *2613* (HNMN, MO, NY); Cerro Musún, above Salto Grande of Quebrada Negra, 500 m, *Neill 1817* (MO). **Río San Juan**: El Castillito–Caño de Oro, Gigante, 10 m, 10°43′15″N, 84°54′30″W, *Martínez 2191* (MO); Caño Chontaleño, 20 km NE of El Castillo, 200 m, *Neill & Vincelli 3608* (BM, CAS, MO). **Rivas**: Isla Ometepe, Volcán Maderas, 600–1000 m, 11°26–27′N, 83°31–32′W, *Robleto 1674* (ENCB, MO); 800–1000 m, 11°26′N, 85°29′W, *2065* (MO). **Zelaya**: El Cerro La Pimienta, ca. 800–1000 m, 13°44′50″N, 84°59′45″W, *Grijalva 396* (CM, HNMN, MO); "Kurinwacito," 80–100 m, 13°08′N, 84°55′W, *Moreno 23753* (MO); 2 km N of Kuikainita, S of Siuna, 100 m, *Neill 4150* (MO); Cerro Livico, 7 km NE of Siuna, 500 m, *Neill 3630* (MO); ca. 13 km above Kururia, road to San Jerónimo, <200 m, *Pipoly 3831* (MO); Cerro Baká, ca. 6.5 km E of Río Coperna, 200–300 m, 13°40′N, 84°30′W, *Pipoly 4918* (MO); Cerro La Pimienta number 1, ca. 900–980 m, ca. 13°45′N, 84°59′W, *Pipoly 5118* (MO); ca. 6.3 km S of Colonia Yolaina, ca. 200–300 m, 11°36–37′N, 84°22′W, *Stevens 6419* (MO); along Caño Majagua, ca. 750–850 m, ca. 13°45′N, 85°00–01′W, *Stevens 6881* (BM, LL, MO); Cerro Saslaya–San José del Hormiguero, ca. 200–400 m, 13°44–45′N, 84°57–58′W, *Stevens 7076* (MO); road to Mina Nueva América, ca. 14.3 km N of El Empalme, *Stevens 8435* (MO); Colonia San José–Tomás Mejía Caño, ca. 40–150 m, ca. 11°53–54′N, 84°20′W, *Stevens 9011* (BM, MO); Bonanza–Constancia, 160–360 m, ca. 13°58′–14°01′N, 84°37–40′W, *Stevens 12466* (MO); ca. 1.5 km NE of Las Esperanza de Las Quebradas, 300–350 m, ca. 13°38′N, 85°02′W, *Stevens & Moreno 19353* (MO); Río Mico, El Recreo, ca. 30 m, *Standley 19749* (F). PANAMA. **Bocas del Toro**: Campamento Changuinola 1, 20 m, *Correa et al. 4067* (MO, PMA). **Coclé**: La Pintada–Coclecito, 5.3 mi. N of Llano Grande, 513 m, *Croat 49240* (MO); 5.6 mi. N of Llano Grande, 1.4 mi. N of Continental Divide, 150 m, 8°46′N, 80°27′W, *Croat 67478* (CM, L, MEXU, MO, PMA); El Valle de Anton, behind Club Campestre, *Croat 14278* (MO). **Darién**: Parque Nacional Cerro Pirre, Alturas de Nique region, near Cana Mine, 500 m, 7°45′N, 77°40′W, *McPherson 11584* (MO); Cerro Pirre region, Cana, 480 m, *Croat 38009* (MO, RSA); 550–760 m, 7°57′N, 77°46′W, *68871* (MO); *68954* (CAS, MO, NY); *Folsom 4417* (MO, PMA); near station along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77107* (MO); Río Paracida, 0–80 m, 8°N, 77°48′W, *Croat 68998* (MO); ca. 13 km E of Pucuro, 450–600 m, 8°03′N, 77°20′W, *Hammel et al. 16195* (MO, US). **Panamá**: El Llano–Cartí, 6.8 mi. N, 350 m, *Croat 49111* (MO).

Philodendron thalassicum Croat & Grayum, sp. nov. TYPE: Panama. Chiriquí: Fortuna Dam area, trail to meteorological station of Río Hornito, ca. 0.5 km S of Centro de Científicos, 1010–1030 m, 8°45′N, 82°18′W, 23 June 1994, *Croat & Zhu 76297* (holotype, MO–4619518–22; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, EAP, F, GB, GH, HUA, IBE, K, LE, M, MEXU, NY, P, PMA, QCA, RSA, S, SCZ, SEL, TEX, U, US, VEN). Figures 408–410, 415.

Planta terrestris aut hemiepiphytica; internodia brevia longa, 2–4 cm diam.; cataphylla 14–46 cm longa, acute 2-costata, persistentia ut fibra; petiolus D-formatus, 38–109 cm longus, 2–14 mm diam., plerumque longior quam laminae; lamina triangulari-sagittata vel ovata, 42–77 cm longa, 16–52 cm lata, atriviridis supra, saepe veneta infra; inflorescentia 1–3; pedunculus 3–14 cm longus, 2–9 mm diam.; spatha 11–20 cm longa; lamina spathae extus alba vel creamea, intus viridalba; tubo spathae 3–7 cm longo, extus pallide viridi, intus virello vel albo; pistilla (4)5–7(8)-locularia; loculi 16–22-ovulati.

Terrestrial or hemiepiphytic, growing to 4 m high in trees; stem appressed-climbing; internodes short, 2–4 cm diam., dark green, semiglossy, drying light yellowish brown, epidermis fragmented, reddish brown; roots several per node, <30 cm long, drying dark brown with epidermis ridged and splitting; cataphylls soft, 14–46 cm long, sharply 2-ribbed (ribs low), green or tinged pink when young to reddish brown or brown, drying brownish, persisting semi-intact, soon dilacerating; **petioles** 38–109 cm long, 2–14 mm diam., D-shaped, firm, flexible, sometimes with low, medial rib adaxially and with adaxial margins obtuse to rounded, medium green, weakly glossy, faintly to conspicuously dark- or striate-lineate, drying yellow-brown, dark brown to sometimes blackened; **blades** triangular-sagittate to ovate-triangular, subcoriaceous, conspicuously bicolorous, acuminate to long-acuminate at apex, sagittate at base, 42–77 cm long, 16–52 cm wide (0.8–1.8 times longer than wide), (0.6–1.4 times longer than petiole), usually shorter than petiole (averaging 0.9 times as long), upper surface dark green, matte or weakly glossy, sometimes glistening, drying dark brown, lower surface much paler (forming an areolate pattern on high magnification) and matte, often bluish green to whitish, drying bluish green if triangular-sagittate or yellowish brown if ovate-triangular, glaucous; anterior lobe 28–58 cm long, 18–51 cm wide (1.6–3.3 times longer than posterior lobes); posterior lobes broadly obtuse to narrowly rounded, 13.5–25 cm long, 10–23 cm wide, rounded; sinus spathulate to parabolic, 9–12 cm deep; midrib broadly sunken to flat above, slightly paler, obtusely triangular and darker below;

basal veins 5–11 per side, with 1–2(3) free to base, with a few veins coalesced for 5–9 cm; posterior rib prominently naked to 2.5–5 cm; primary lateral veins (4)12–18 per side, departing midrib at a 50–60° angle, weakly arcuate to ± straight to the margins, C-shaped to sunken and slightly paler above, convex and concolorous below; minor veins conspicuous, darker than surface to obscure below, arising from both the midrib and primary lateral veins. INFLORESCENCES ± erect, 1–3 per axil; peduncle 3–14 cm long, 2–9 mm diam., coarsely white-striate; **spathe** 11–20 cm long (1.15–2.8(4.7) times longer than peduncle); spathe blade white to cream and densely short-lineate outside, greenish white inside; spathe tube pale green and short-lineate outside, 3–7 cm long, greenish to white, sometimes faintly pinkish inside; **spadix** sessile to weakly stipitate; 12.8–16.6 cm long; pistillate portion 5.5 cm long in front, 3–3.5 cm long in back, 1.6–2 cm diam. midway, 1.5–1.6 cm diam. ca. 1 cm from apex; staminate portion 6.8–9.4 cm long; fertile staminate portion tapered toward apex, constricted (to 8–10 mm, 1.5–2 cm above base of sterile section) above sterile male flowers, 1 cm diam. at base, 1–1.6 cm diam. at middle, 5–7 mm diam. near apex; sterile staminate portion 1–1.7 cm diam. at base, 1 cm diam. at apex; pistils 2.8–3.8(6.2) mm long, 1.2 mm diam.; ovary (4)5–7(8)-locular, 1.7–2.3 mm diam., with axile placentation, wall sometimes embedded with angular crystal-like particles; locules 2.7(4.9) mm long, 0.5–0.6 mm diam.; ovules ca. 16–22 per locule, 2-seriate, 0.2–0.4 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition; stigma lobed; style 1.3–2.1 mm diam., similar to style type B; style apex sloping to somewhat rounded, drying granular with an acute, turned up margin; stylar pores thickened, usually fused with the crown, sometimes free or nearly so, each with its own fringe of stigmatic papillae; style boss broad, shallow to quite shallow; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 0.9–1.2 mm long; thecae oblong, ± parallel to one another; sterile staminate flowers prismatic to weakly clavate, irregularly 5–6-sided, 1.2–1.6 mm long. INFRUCTESCENCE with berries whitish (maturing).

Flowering in *Philodendron thalassicum* occurs throughout the dry season to the mid-rainy season (January through August), though no flowering collections are known from Feburary (although post-anthesis collections do exist). Post-anthesis collections are known from April and May, and especially June, July, and August, and also from November (indicating that flowering may occur later than August). Immature fruiting collections are known from January, February, June, September, and November.

Philodendron thalassicum ranges from central Costa Rica to western Panama (Chiriquí) at (775)1000 to 2100 m elevation in *Premontane rain forest*, *Tropical Lower Montane wet forest*, and *Tropical Lower Montane rain forest* life zones.

Philodendron thalassicum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Impolita.* This species is characterized by its short thick internodes, two-ribbed cataphylls persisting as fibers, more or less D-shaped petioles (averaging longer than the blades), internally greenish to white spathe tube, and especially by the pale matte, often bluish green lower leaf surfaces. The epithet "thalassicum" (from thalassicus, meaning sea green or bluish green) is derived from this coloration of the lower blade surface.

Philodendron thalassicum may be confused with *P. hebetatum* and *P. strictum*, which also have matte, much paler lower blade surfaces. Both differ in having subterete petioles drying conspicuously light yellow-brown, rather than sharply D-shaped and drying somewhat blackened as in *P. thalassicum.* In addition, both *P. hebetatum* and *P. strictum* have cataphylls drying yellowish and semi-intact and spathe tubes colored reddish, maroon, or violet-purple within.

Plants of *P. thalassicum* with sagittate blades might be confused with narrow-leaved plants of *P. jodavisianum* or *P. tenue*, but both of those species have blades that are semiglossy to glossy (not at all glaucous) below. More ovate blade-forms of *P. thalassicum* might be confused with *P. schottianum*, but the latter also usually has a semiglossy lower blade surface, cataphylls that persist semi-intact, and spathe tubes reddish internally.

Philodendron thalassicum is variable in blade shape, with some triangular-sagittate (e.g., *Grayum et al. 3760, Croat 15876, 15745*) and others ovate (e.g., *Burger & Burger 7541, Burger & Stolze 5661, Burger & Liesner 6745*). Those with ovate leaves sometimes dry brownish on the lower surface while those with the triangular-sagittate blades dry bluish green. No other differences between these two forms have been detected.

Additional specimens examined. COSTA RICA. **Alajuela**: Cantón Alfaro Ruiz, Tapesco de Zarcero, 1650 m, *A. Smith NY1232* (F, NY); Alto Palomo, 1900 m, *Lent 1844* (CR, F); Naranjo–Quesada, along Hwy. 15, 3.2 mi. N of Zapote, 1560 m, *Croat 46908* (MO); Cantón San Ramón, R. B. Monteverde, Cordillera de Tilarán, valle del Río Peñas Blancas, 1600 m, 10°19′15″N, 84°46′30″W, *Bello 5151* (CR, INB, MO, NY); Monteverde reserve, 10°20′N, 85°50′W, *Croat 61191* (cultivated) (MO). **Car-**

tago: Moravia, 3.5 km from Finca Racine, 1200–1300 m, *Croat 36634* (CR, MO); Moravia de Chirripó–Turrialba, 1400–1600 m, *I. Chacón 269* (MO); Río Dos Amigos–Río Villegas, W of Río Grande de Orosi, ca. 1650 m, 9°42′N, 83°47′W, *Grayum et al. 3760* (MO, RSA); Quebrada Honda–Río Sombrero, ca. 1–2 km above El Muñeco, ca. 1400 m, *Luteyn 3238* (DUKE); ca. 20 km E of Río Pacuare, on road toward Moravia, 1150 m, 9°50′N, 83°24′W, *Thompson & Rawlins 1234* (CM); Quebrada Cangreja, 3 km S of Pan-American Highway, 1620–1650 m, 9°46′N, 83°57′W, *Liesner & Judziewicz 14498* (CR, MO); Tapantí Hydroelectric Reserve, ca. 1 km S of junction of Quebrada Salto and Río Grande de Orosi, 1500–1800 m, 9°43′N, 83°47′W, *Croat 36211* (MO); 1500–1700 m, *36078* (MO); 1525–1595 m, *79049* (CR, INB, MO); *Croat & Grayum 68290* (MO, US); *Grayum & French 5821* (INB, MO); 1600 m, *Lent 964* (CR, F, US); 1500 m, 9°42′N, 83°47′W, *Burger & Liesner 6745* (F, US); 1600 m, 9°42′N, 83°47′W, *Burger & Stolze 5661* (CR, DS, F, WIS); 5,200 ft., *Utley & Utley 7284* (MO); 1400–1700 m, *5184* (DUKE, MO); ca. 1600 m, 9°42′N, 83°46′W, *Burger & Burger 7541* (F, MO); 1400–1600 m, 9°42′N, 83°47′W, *Baker & Utley 201* (F, MO); Río Navarro, El Muñeco, 1400–1500 m, *Standley & Torres 51371* (US). **Heredia**: 4 mi. N of Vara Blanca, 1350 m, *Croat 35595* (MO); *35621* (MO); 9 km SE of San Ramón [de Sarapiquí], 1000 m, 10°16′N, 84°05′W, *Loiselle 138* (MO); Paracito–Río Claro, vic. of Bajo La Hondura, 1100–1400 m, *Croat 44500* (MO); Parque Nacional Braulio Carrillo, San Rafael de Vara Blanca, 1830 m, 10°11′50″N, 84°06′35″W, *Herrera 246* (MO); Sarapiquí, 1750 m, 10°12′47″N, 84°06′05″W, *Boyle & Boyle 2695* (MO); Finca Montreal, between headwaters of Río Volcán and Río San Fernando, 1800 m, 10°12′39″N, 84°06′45″W, *Boyle 1084* (CR, MO); Volcán Barva, Río Peje–Río Sardinal, Atlantic slope, 1200–1400 m, 10°15′30″N, 84°05′W, *Grayum & Herrera 7846* (MO); Río San Rafael, 1500 m, 10°13′N, 84°05′W, *Grayum 7050* (MO). **Limón**: Cordillera de Talamanca, Kamuk massif, 1900–2300 m, 9°14–15′N, 82°59′W, *Davidse & Herrera 29201* (MO). **Puntarenas**: Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, 1200 m, 8°49′N, 82°58′W, *Croat 57264* (CR, MO); Río Coto Brus, near Cotón, 23 km N of La Unión (on Panama border), *Croat 26685* (CR, MO); Cerro Frantzius–Cerro Pittier, around Río Canasta, 9.5 airline km NW of Agua Caliente, 1500–1600 m, 9°02′N, 82°59′W, *Davidse et al. 28365* (CR, MO, NY); Quebrada Kuisa, near crossing of Ujarrás–San José Cabécar trail, 2100 m, 9°20′30″N, 83°14′W, *Grayum 10282* (CR, INB, MO); Monteverde Reserve, 1500 m, 10°17′N, 84°48′W, *Hammel et al. 14206* (MO); 1500–1600 m, 10°18′N, 84°47′W, *Haber & Zuchowski 10020* (CR, INB, MO, MV); 1500–1620 m, *Pounds 334* (CM, MO); *357* (MO); 1450–1650 m, *Burger & Baker 9772* (F, MO); Cerros Centinelas, 1550–1600 m, 10°18′N, 84°47′W, *Grayum & Sleeper 3857* (CR, MO). **San José**: trail beyond Bajo La Hondura, towards Río Claro, 1100–1200 m, *Luteyn 3318* (DUKE, MO); NE slope of Altos Tablazo, between Quebrada Tablazo and summit of ridge, 1700–1875 m, 9°50′N, 84°02′W, *Grayum & Schatz 5181* (CR, MO); Parque Nacional Braulio Carrillo, Estación La Montura, *Gómez et al. 20827* (CR, MO); General Valley, 1500 m, 9°27′N, 83°43′W, *Burger & Barringer 11601* (F, MO); Cerro Hondura, between Río Patria and Río Zurquí, 1500–1600 m, 10°04′N, 84°01′W, *Grayum & Sleeper 6131* (CM, MO). PANAMA. **Chiriquí**: NW side of Cerro Pando, *Croat 15966* (MO); Fortuna Lake area, along Continental Divide, 1200 m, 8°44′N, 81°17′W, *Croat 74975* (L, MO, NY, PMA, QCA); Río Hornito–Río Chiriquí, 1050–1100 m, ca. 8°44′N, 82°13′W, *Stevens 18371* (MO); Boquete region, Monte Rey, *Croat 15876* (MO), *15745* (MO); SW slope of Cerro Pate Macho, 1630–1780 m, 8°46′N, 82°25′W, *Croat 66401* (CAS, F, K, MBM, MO, TEX, W); Quiel road, 10 km above Boquete, 5500 ft., *Proctor 31831* (LL); Río Palo Alto–Cerro Pate Macho, ca. 6 km NE of Boquete, 1600–1700 m, 8°48′N, 82°23.5′W, *Grayum et al. 6359* (MO, PMA, US); Cerro Horqueta, ca. 1650 m, *Croat 27000A* (MO).

Philodendron tripartitum (Jacq.) Schott, Wiener Z. Kunst 1829: 780. 1829. *Arum tripartitum* Jacq., Pl. hort. schoenbr. 2: 33, t. 190. 1797. *Caladium tripartitum* (Jacq.) Willd., Sp. pl. 4: 491. 1805. TYPE: t. 190 in Jacq., Pl. hort. schoenbr. 1797 (holotype). Figures 411, 412, 416–424.

Philodendron fenzlii Engl., in Mart., Fl. Bras. 3(2): 144. 1878. TYPE: Mexico (holotype, B? lost). Schott ic. 2599 (neotype, here designated, W).

Philodendron affine Hemsl., Diagn. Pl. Nov. Mexic. 37. 1879. TYPE: Guatemala. Barranca Honda, Volcán de Fuego, *Salvin s.n.* (holotype, K).

Philodendron tripartitum var. *tricuspidatum* Engl., in Mart., Fl. Bras. 3(2): 144. 1878. TYPE: Costa Rica. San José: 1300 m, May 1857, *C. Hoffmann s.n.* (B? not seen).

Hemiepiphytic; appressed-climbing, stem often several meters long, sap watery, very aromatic-scented; internodes moderately elongate except near the apex, semiglossy, drying coarsely and irregularly ribbed (the ribs usually acute), 3–14 cm long, 1–2 cm diam. (to 3.5 cm diam. in Colombia), green to dark green to gray-green, soon drying light brown, epidermis sometimes loose and papery, roots usually 3–6 per node, usually less than 20 cm long, drying brown, less than 3 mm diam., semiglossy, sparsely scaly; cataphylls thin, (10)18–33 cm long, usually unribbed, sometimes sharply 1-ribbed, greenish, sometimes tinged reddish, deciduous intact. LEAVES erect-spreading to spreading; **petioles** 20–61 cm long, 6–15 mm diam., terete to subterete, moderately spongy, sometimes obtusely somewhat flattened, sometimes with an obtuse medial rib, dark green, surface glossy to weakly glossy; **blades** deeply 3-lobed almost to the base or rarely trisect, ca. as broad as long in outline, thinly coriaceous, semiglossy, moderately bicolorous, acuminate at apex, lower surface sometimes heavily tinged purplish or reddish; typically rather dissimilar, median segment usually oblanceolate, sometimes nearly elliptic, rarely oblong to linear, 15–45 cm long, (4.5)7–14(19) cm wide, 1.9–7.8 times longer than wide (averaging 4.3 times longer than wide), ((0.9)1.5(1.7) times longer than lateral segments); the lateral segments conspicuously ine-

quilateral, arcuate-spreading toward apex, (12)18–35 cm long, 1.3–15 cm wide, the inner margin always much narrower than the outer margin and weakly confluent with medial lobe, usually to 1 cm, rarely to 2 cm, the outer margin 1.5–5 times wider than the inner margin where the difference is most severe; midrib broadly convex, concolorous above, convex to round-raised, darker below; basal veins lacking; primary lateral veins (4)6–10(12) per side, departing midrib to a 25° angle on narrow blades or to 90° angle on broader blades, weakly curved on narrow blades or markedly curved on broader blades to the margins, sunken and usually concolorous above, convex and darker than surface below; minor veins fine and conspicuously visible, arising from both the midrib and primary lateral veins. INFLORESCENCES usually solitary, sometimes 2–3 per axil; peduncle 3–16 cm long, 6–13 cm diam., medium green, moderately recurved with reddish ring around the apex; **spathe** (8)13–21 cm long, 1.2–4 cm diam., weakly constricted above the tube, to 2.5 cm diam. at constriction, usually medium green to yellow-green, rarely creamy white, with dark purple dots (most to 3 mm circumference) heavily so on tube, less so on blade throughout, white to creamy white or greenish white within, cucullate at apex, convolute in lower ⅔ of tube at base, margins whitish or colorless, recurled at anthesis; spathe blade glossy, smooth outside, (the opening 7.5–8.5 cm long, 3.4–5.2 cm wide), creamy white, glossy; resin canals intermittent, orange, appearing medially and extending into spathe tube inside; spathe tube oblong, glossy outside, 5 cm long, 3 cm diam., maroon, deep red, or purplish-violet inside; **spadix** sessile or shortly stipitate (to 2 mm); clavate, ± erect, 12.3 cm long, broadest above the middle, weakly constricted between sterile and fertile portions; pistillate portion greenish white to pale yellowish green, 2.5–4.5(6.2) cm long, 1–1.8 cm diam. throughout; staminate portion 7.5–8.5 cm long; fertile staminate portion creamy white, 1.2 cm diam. at base, 1.3 cm diam. at middle, 1 cm diam. ca. 1 cm from apex, broadest in the middle, usually narrower than the pistillate and sterile portions; sterile staminate portion usually broader than the pistillate portion, creamy white, drying yellowish, 1.3 mm diam.; pistils 1.7–2.5(3.4) mm long, 0.6–1.1(2.3) mm diam.; ovary 6–8(10)-locular, 0.8–2.3 mm long, 1.1–2.3 mm diam., with sub-basal placentation; locules 0.8–1.1(2.3) mm long, 0.2–0.4(0.7) mm diam.; ovule sac 0.7–0.9(1.2) mm long; ovules 1–2 per locule, contained within a translucent and gelatinous matrix, 0.4–0.6 mm long, longer than funicle; funicle 0.2–0.4 mm long (can be pulled free to base), style 0.4–0.8 mm long, 1–1.4(2.5) mm diam., usually similar to style type D (rarely B or E); style apex ± rounded; stigma subdiscoid, truncate, 0.7 mm diam., 0.2–0.3 mm high, covering center of style apex, inserted on style boss; the androecium truncate, prismatic, margins usually irregularly 5-sided, 1.4 mm long, 2.2 mm diam. at apex; thecae oblong, 0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, prismatic, irregularly 4–6-sided, 1.9 mm long, 1.5–2 mm wide. Berries whitish, irregularly angular, 4 mm long, 2–2.7 mm diam.; seeds usually 6–8 per berry, cylindrical, 1.5 mm long, sticky. JUVENILE plants with blades maroon below.

Flowering in *Philodendron tripartitum* occurs throughout the dry season and the first half of the rainy season (mostly May through July), with seemingly little phenological variation throughout its range. Most flowering collections have been made from January through July with a few from August and also November. Post-anthesis inflorescences have been collected throughout the whole year with the greatest concentration from May to July. Immature fruits are known from January, April, July, August, September, and November, while mature fruits are known only from October.

Philodendron tripartitum ranges from Mexico to Ecuador from near sea level to 1300(1500) m elevation. In Central America, this species ranges along the Caribbean slope in Mexico (Veracruz to Tabasco) and throughout Middle America, but occurs on both slopes in Costa Rica and Panama thence along the Pacific slope into lowland Antioquia and Chocó Departments, Colombia. In Mexico, *Philodendron tripartitum* occurs in Selva Alta Perennifolia and the transition forest to Bosque Caducifolia. In Costa Rica and Panama, it occurs in *Tropical moist forest* to *Premontane wet forest, Tropical wet forest,* and *Premontane rain forest.* In Colombia, it is known from *Tropical wet forest* and *Tropical rain forest.*

Philodendron tripartitum is a member of *P.* sect. *Tritomophyllum.* This species is characterized by its elongate internodes, deeply trilobate leaf blades only weakly confluent at the base or sometimes completely trisect, and spathes scarcely constricted above the tube.

Philodendron tripartitum is most likely confused with the common *P. anisotomum.* See under the latter species for the differences. It is probably most closely related to *P. cotobrusense* from Costa Rica, which differs in having elliptic medial lobes with 18 or more pairs of primary lateral veins. *Philodendron tripartitum* may be confused also with *P.*

madronoense from Panama. That species also differs in having elliptic medial lobes with about 25 pair of primary lateral veins.

Along with *P. sagittifolium*, *P. tripartitum* is one of the most highly variable and widespread species in the genus, with complex patterns of variation in the shape of the lobes, the degree to which the lobes are confluent, the number of primary lateral veins, and the size and number of inflorescences per axil. Clinal variations range both north and south throughout Mexico and Central America and also elevationally. Most Mexican specimens have the lobes conspicuously confluent at the base with the lateral lobes moderately to prominently auriculate, and all have one inflorescence per axil. This form is well characterized by Engler's drawings of Araceae Drawing no. 48 of the synonym, *P. fenzlii*. In Mexico, *P. tripartitum* ranges from sea level to usually about 900 m elevation.

To the south and east in Central America, especially at lower elevations, the blades of *P. tripartitum* dry paler green and are more weakly confluent at the base or completely trisect with the lateral lobes only weakly auriculate. This form is encountered in eastern Chiapas and Tabasco and ranges through Belize and the remainder of Caribbean coastal Central America, as well as on the Pacific coast of El Salvador. It reaches its most deeply trisect and pale green expression in *Tropical Moist forest* along the Caribbean coast of Panama, but also at lower elevations along the Pacific slope in Darién Province. In contrast to material from Mexico and Belize, this form of the species generally has but a single inflorescence per axil, though in Panama it may have from one to three inflorescences per axil. Noteworthy collections of this form are *Dressler 1513* and *Breedlove 10330* from eastern Chiapas, which have blades drying pale yellow-green and weakly confluent with only weakly auriculate lateral lobes, yet occur at between 950 and 1266 m (3800 ft.) elevation.

Most collections of *P. tripartitum* from above 500 m and from wet life zones (e.g., *Premontane wet forest* and *Tropical wet forest*) in Nicaragua, Costa Rica, and western Panama (Chiriquí Province) have typically dark-drying blades with moderately confluent and auriculate lateral lobes. Collections from the highlands of Nicaragua and Costa Rica may have one to three inflorescences per axil, and each inflorescence is typically smaller than when but a single inflorescence is present.

Collections from lowland southwestern Costa Rica on the Pacific Coast differ from those of lowland Pacific coastal Panama and El Salvador in having the lobes more broadly confluent; more prominently auriculate lateral lobes; broader medial lobes, with more numerous primary lateral veins; and in often drying more yellowish brown. Particularly noteworthy is *Davidse 24202* from the Costa Rican highlands southeast of Las Alturas. It has comparably broadly convolute lateral lobes and approaches *P. cotobrusense* in having medial lobes with closer, more numerous primary lateral veins and five inflorescences per axil. It is conceivably a hybrid with that species.

Collections from central Panama, especially El Valle and the vicinity of Cerro Jefe, exhibit extreme variation in leaf morphology and even spathe coloration. This is true to a lesser extent elsewhere in Panama, at Santa Fe, along the El Llano–Cartí Road, and on the Santa Rita Ridge Road. In Coclé, typical plants have somewhat blackened leaf blades with slender, weakly auriculate and weakly confluent lobes. These collections have the medial lobe ranging from 4.4 to 7.2 times longer than wide. This same narrow-lobed variation occurs also on Cerro Jefe and the Santa Rita Ridge Road where the lobes may be proportionately even more slender, ranging from 7.3 to 13 times longer than wide. Two collections from the El Llano–Cartí Road, *Thompson 4704* and *Miller et al. 862*, have somewhat larger blades with the medial lobes five to six times longer than wide. These narrow-leaved forms vary from having 1–2 relatively large inflorescences per axil (*Luteyn 4066*) or with up to three smaller inflorescences per axil (*Gentry 7433*). The spathes are variously reported as reddish green or red-brown, to pink, red, or purple.

Spathe color is not variable throughout most of Central America, where the spathe tube is generally green outside but maroon in the lower two-thirds within. Spathe color becomes more variable in Panama, where in the narrow-lobed forms (mentioned above) it may be reported as purplish or red. As one approaches South America, spathe color becomes more variable. In eastern Panama at the Serranía de Majé and in Darién Province, the spathe is reported as green mottled purple (*Whitefoord & Eddy 223*) or yellow-green with purple flecks (*Churchill & de Nevers 4480*), or even cream with red spots (*Knapp & Mallet 3160*). There seems to be no correlation with either elevation or the degree to which the lobes are confluent or auriculate.

Style type in *P. tripartitum* is also variable. Throughout most of its range, from Mexico to Panama along the Caribbean coast, the style is raised and button-shaped (Mayo style type D). Generally, the stylar canals emerge onto the surface near the outer margin of the style through moderately large pores on a generally flattened apex. However, some

collections, notably *Grayum et al. 5034* from 600 m in Heredia Province in Costa Rica, have pores somewhat pie-shaped and the general level of the apex somewhat sunken. More extreme manifestations of this phenomenon are present in *Grayum 6979* (studied in reconstituted condition), from Heredia Province at 700–900 m and *Croat & Porter 16241*, from Bocas del Toro Province, Panama, near sea level. In these collections the style type might more appropriately be referred to as a Mayo style type E since it is definitely funnel-shaped with a distinct marginal rim. In *Grayum 6979* the style is broadly bowl-shaped with moderately large pores situated about midway between the annulus and the center. In *Croat & Porter 16241* the funnel is held above the surface of the style in dried condition, with the margins curled under, and there are radial ribs on the inside of the funnel just as there are in the *Grayum et al. 5034* collection. It is also similar to the latter collection and the remainder of the type D styles in having large pores positioned along the outer edge of the nearly straight-walled funnel. Indicating that these style types are probably merely variations of the D-type style is the fact that *Gómez et al. 21988* from the highlands of Puntarenas Province has both extremes of style types represented on both of the above-mentioned collections.

Three other style types are also present in *P. tripartitum* and may ultimately allow separation of distinct subspecies because they occur in more isolated populations. One of these is Mayo style type E, represented by specimens collected from the Pacific slope of Costa Rica, e.g., *Croat 35248* from San Isidro–Dominical Road at 1000 m, and *Burger & Stolze 5473* from Rincón de Osa. In this type of style the stylar pores are smaller than in type D and are arranged in a smaller circle at the base of the funnel. Similar to the material from southwestern Costa Rica in this respect is a collection from Darién Province, Panama, near the Colombian border (*Whitefoord & Eddy 223*).

The second novel type of style is present on collections from higher elevations in Panama, e.g., *Croat 66228* from Chiriquí Province and *Croat 69721* from Darién Province. This style type is perhaps sufficiently different to warrant the recognition of these collections as a distinct subspecies. It is similar to Mayo style type B, except that the style is weakly sunken rather than flattened. The stigmatic papillae may cover the entire concave area or they may arise primarily from the center. The stylar pores are smaller than in style type D, and are arranged in a tight circle at the center of the funnel, much as in the case of style type E in southwestern Costa Rica. In this case, however, there is no sign of a protruded funnel, so apparent on collections from the latter area.

While the style types mentioned here seem to warrant recognition of two or more subspecies in *P. tripartitum*, the highly variable general morphology of the species and the general state of preservation of the ovaries of most collections precludes the thorough analysis needed.

Standley and Steyermark (1958a) reported the fruits of *P. tripartitum* as red, but this is unsubstantiated. Bunting (1965) stated that the locules are strictly 1-ovulate, whereas Standley and Steyermark (1958a) described them as 1–3-ovulate. Bunting's findings have here been confirmed.

Many of the variations discussed above, if considered in isolation, are distinctive and would appear to be worthy of recognition. However, considering the immense variation within populations, the overlapping characteristics, and the generally similar structure of the flowers, it seems best to consider this group a single but highly variable species.

This species was reported in Jacquin's (1797) original description for Venezuela, but it does not occur there. Since the type illustration (t. 190) clearly represents this species it must be presumed that Jacquin, who apparently described the plant from a cultivated collection, must have been confused about the origin of the material. Schott (1829), who transferred *Arum tripartitum* to *Philodendron*, claimed to have seen only living material, perhaps the same collection seen by Jacquin at Schönbrunn. Bunting (1979) excluded *P. tripartitum* from his treatment of the Araceae for Venezuela and used the name *P. holtonianum* Schott for a Venezuelan species with three-lobed species. The Jacquin plate (t. 190) clearly does not match *P. holtonianum*, which differs in having the lateral lobes more broadly confluent and not at all auriculate at the base with the posterior rib naked 3 to 5 cm at the base. In contrast, leaves of *P. tripartitum* are often noticeably auriculate with the posterior rib not at all naked. Krause (1913) treated *P. holtonianum* as a variety of *P. tripartitum* but these species, while superficially similar in blade shape, are probably not closely related.

Caladium trifoliatum Desf. was questionably included by Krause as a synonym of this species, but the description is of a plant with the lateral lobes petiolulate, whereas leaf blades in *P. tripartitum* are at most trisect, with the lateral lobes sessile.

Additional specimens examined. BELIZE. **Cayo**: *Lundell 6336* (CM, MICH); McCaw River–Cuevas, vic. of Milonario, 1900 ft., *Croat 23670* (MO). **Stann Creek**: Mid-

dlesex, *Gentle 2936* (CM, MICH). **Toledo**: Edwards Road beyond Columbia, *Gentle 6217* (LL); Jacinto Creek, *Gentle 6002* (LL); Monkey River, Monkey River–Cockscomb, *Gentle 4458* (LL, MICH); Punta Gorda, 1 mi. E of junction with road to San Antonio, 100 ft., *Croat 24509* (MO); SW Maya Mountains, Columbia River Forest Reserve, trail between Union and Gloria Camps, 700–750 m, 16°23′22″N, 89°08′10″W, *Holst 4388* (MO); Southern Maya Mountains, Bladen Nature Reserve, 260 m, 16°30′15″N, 88°55′07″W, *Davidse 35794* (BRH, MO). COSTA RICA. **Alajuela**: 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, 10°28′N, 84°30′W, *Liesner 14121* (B, CR, MO); Río Peñas Blancas, below Monteverde Cloud Forest Nature Reserve, 1250–1350 m, 9°17′N, 84°86′W, *Burger et al. 10770* (CHAPA, NY); 850 m, *Bello 362* (CR, MO); 700–900 m, *Haber & Zuchowski 9468* (CR, MO); San Ramon, 820 m, 10°19′N, 84°43′W, *Bello & Eyol 2684* (INB, MO); 840 m, *Bello et al. 10870* (CR, INB); 15 km N of Boca Arenal, ca. 100 m, 10°38′N, 84°31′W, *Liesner et al. 15043* (CR, MO); Cañas–Upala, 13.8 km N of Bijagua, 100–150 m, *Croat 36447* (MO); 4 km NNE of Bijagua, ca. 400 m, *36253* (MO); Upala, 550 m, *Garcia 187* (CR, INB); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, *Croat 43593* (MO). **Cartago**: Turrialba, *Cook & Doyle 378* (US); Moravia–Quebrada Platanillo (Tsipirí), ca. 1250 m, *Croat 36659* (MO); 4 km SE of Pejibaye along Río Gato, 700 m, 9°48′N, 83°42′W, *Liesner 14342* (CR, MO). **Guanacaste**: Volcán Miravalles, ca. 800 m, 10°42′N, 85°07′W, *Burger & Gentry 9127* (CR, F, U); Parque Nacional Rincón de la Vieja, Volcán Santa María, 900–1200 m, 10°47′N 85°18′W, *Davidse et al. 23313* (CR, MO); 840 m, *Rivera 479* (CR, MO). **Heredia**: La Selva Field Station, 100 m, *Grayum 3019* (DUKE); *3033* (DUKE); *2444* (DUKE); 100 m, *2863* (DUKE); *Croat 44227* (MO); *Grayum & Sperry 2212* (DUKE); *Sperry 982* (DUKE); *Folsom 10011* (DUKE); Quebrada Tigre–Río Sardinal, ca. 9 km SW of Las Horquetas, ca. 600 m, 10°17′N, 84°02′W, *Grayum et al. 5034* (MO); Volcán Barva, 700–950 m, 10°17′30″N, 84°04′30″W, *Grayum 6979* (MBM, MO, W); Route 9, 3 km S of La Virgen de Sarapiquí, 200 m, *Woodruff 188* (FLAS); 9 km SE of San Ramón, 1000 m, 10°16′N, 84°05′W, *Loiselle 161* (MO); San Ramón, *Tonduz 17719A* (K, P). **Limón**: ca. 4–5 airline km S of Islas Buena Vista in the Río Colorado, 100–180 m, 10°38′40″N, 83°41′W, *Davidse & Herrera 31293* (CR, MO); Hitoy Cerere reserve, SW of Valle La Estrella, 150–550 m, 9°39′N, 83°02′W, *Grayum et al. 5809* (MO); 2 km W of Río Toro Amarillo, W of Guápiles, 275 m, 10°13′N, 83°50′W, *Thompson & Rawlins 1217* (CM); Hone Creek–Cahuita, *Gómez et al. 20523* (MO); ca. 1 km N of Shiroles, ca. 50 m, *Croat 43277* (MO); ca. 10 mi. S of Punta Cahuita, ca. 3 mi. S of turnoff to Bribrí, ca. 70 m, *Croat 43202* (MO); vic. Laguna Pereira, 2–4 m, 10°47–49′N, 83°37′W, *Stevens et al. 25184* (MO); Guápiles, 850 ft., *J. D. Smith 4981* (US); 30 m, *Robles 2241* (CR, MO); Los Angeles, San Miguel, 1100 m, 10°06′40″N, 83°59′40″W, *Herrera & Schik 3826* (CR, INB, MO); Parque Nacional Tortuguero, 40 m, 10°28′N, 83°34′W, *Robles 1738* (CR, MO). **Puntarenas**: Cordillera de Talamanca, 2160 m, 9°20′20″N, 83°13′55″W, *Bittner 1787* (INB, MO); Parque Nacional Corcovado Estación Sirena, sea level, 8°28′N, 83°35′W, *Knapp 2189* (F, MO, NY, US); 1–50 m, *Kernan & Phillips 1090* (CR, MO); 220 m, 8°34′N, 83°31′W, *Aguilar 2848* (CR, INB); Rincón de Osa, 20–150 m, *Liesner 1991* (MO, US); Fila El Tigre, SE of Las Alturas, 1350–1450 m, 8°56′N, 82°51′W, *Davidse 24202* (B, MO); Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, 1500–1600 m, 9°02′N, 82°59′W, *Davidse et al. 28422* (CR, MO); Osa Península, Rancho Quemado, ca. 15 km W of Rincón, 200 m, 8°40′N, 83°34′W, *Hammel et al. 16981* (CR, MO); Chacarita–Rincón de Osa, 10 km W of Chacarita, ca. 100 m, 8°45′N, 83°18′W, *Croat & Grayum 59881* (MO); Osa, Agua Buena, 60–70 m, 8°41′32″N, 83°30′21″W, *Ramírez 223* (CR, MO); vic. Rincón de Osa, 50–200 m, 8°42′N, 83°31′W, *Burger & Gentry 8922* (F); 20–60 m, *Utley & Utley 1234* (F, MO); 30 m, 8°42′N, 83°31′W, *Burger & Stolze 5473* (CR, F, US); Quebrada Vaquedano, 500 m, 8°38′45″N, 83°35′25″W, *Herrera 4013* (CR, MO); La Tigra–Las Mellizas, 1280 m, *Gómez et al. 21988* (MO); Palmar Norte, trail to Jalisco, 50–700 m, *Croat 35193* (MO); 6 km S of San Vito de Java, ca. 5000 ft., *Raven 21852* (CR, DH, DS); Río Bella Vista near Las Alturas, 1300 m, 8°56′N, 82°51′W, *Lent 2686* (CR, F); Finca Las Alturas, at Cotón, Río Cotón, ca. 1300 m, *Croat 44362* (MO); La Unión–Cotón, Río Negro–Río Coto Brus, *Croat 26582* (MO); Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1150 m, *Croat 22295* (MO); Burica Peninsula, Quebrada Palito, 20–270 m, *Croat 22617* (MO). **San José**: El General Valley, vic. of San Isidro El General, 730 m, *Molina et al. 18308* (EAP, F, NY, US); San Isidro del General–Dominical, above Alfombra, 1000 m, 9°18′N, 83°46′W, *Burger & Baker 10113* (F); 990–1100 m, *Croat & Hannon 79108* (INB, MO); 2 km N of Dominical along CR-223, 40–100 m, *Utley & Utley 4944* (DUKE); ca. 4.5 mi. SW of Canaán road from Rivas, ca. 900 m, *Croat 43438* (MO), *43446* (MO); 9 mi. SW of Río Pacuar, 680 m, *Croat 35342* (MO); SW of San Isidro, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35248* (MO). EL SALVADOR. Jardín Botánico, Zona 23SC, 800 m, 13°40′N, 89°15′W, *Villacorta 317* (LAGU, MO). GUATEMALA. **Alta Verapaz**: near Finca Sepacuite, *Cook & Griggs 743* (US); Chamá, *Johnson 404* (CM, US); Cubilqüitz, 350 m, *Tuerckheim 8023* (US); *J. D. Smith 8023* (US); Pantín, below Tamahú, 600 m, *Standley 70543* (F); 4 mi. up road to Oxec, N off Highway 7E, ca. 6 km NE of Panzós, 500 m, *Croat 41610* (MO); 9 mi. up road to Oxec, 800 m, *41684* (MO). **Izabal**: near Entre Ríos, 18 m, *Standley 72745* (F). **Petén**: Dolores, km 83, Machaquila Road, *Contreras 2115* (LL). HONDURAS. **Atlántida**: Lancetilla Reserve, near Tela, 70–150 m, 15°44′N, 87°27′W, *Croat 42670* (MO); *Croat & Hannon 64640* (MO, NY); *Standley 53381* (F, US); S of San Alejo near Río San Alejo, 150–270 m, *Standley 7962* (F); ca. 10 km SW of La Ceiba, 80–150 m, 15°42′N, 86°51′W, *Liesner 26077* (MO). **Gracias a Díos**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9181* (MO, UNAH); Río Plátano, 84°40–85′N, 15°30–55′W, *Clewell & Cruz 4062* (CHAPA, MO, UC). **Morazán**: vic. El Zamorano, 800 m, *Molina 34354* (MO). **Yoro**: Texíguat River, 1 km SW of San José de Texíguat, 100–400 m, 15°30′N, 87°26′W, *Hazlett & Brant 8047* (MO); Río Guán Guán, ca. 3 km S of San José de Texíguat, 380 m, 15°30′N, 87°27′W, *Evans 1323* (MO). MEXICO. **Chiapas**: 27–43 km SW of Palenque, 210–810 m, *Croat 40335* (MO), *40306* (MO); 460 m, *Croat 40269* (MO); 20 mi. N of Ocozocoautla, 700 m, *Croat 40634* (MO, NY); 13 mi. N of Ocozocoautla, 900 m, *Croat 40620* (MO, NY); Mpio. Cintalapa, Oaxaca–Chiapas border, 4 km W of La Ciénega, 38 km W of Las Cruces, 1400 m, *Breedlove 25132* (MO); 5 km W of Bonampak, 350 m, *Martínez 6972* (MO); 2 km NE of Bonampak above Cojolite, 350 m, *7939* (MO); Laguna Ocotal Grande, 45 km E of Ocosingo, *Dressler 1513* (GH, US); 10 mi. N of Ocozocoautla, 3800 ft., *Breedlove 10330* (F); km 18 on road to Malpasco (N of Ocozo-

cautla), 2700 ft., *Kennedy 1426* (SEL); Bochil–Pichucalco, 17.1 km SW of Pichucalco, 430 m, *Croat 78662* (CHIP, MO). **Oaxaca**: Uxpanapa region, 17 km E of Sarabia, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63212* (B, BM, K, MO, NY, US); 150 m, 17°33′N, 92°59′W, *65367* (MO); Tuxtepec–Oxaca, 6 mi. W of Valle Nacional on Highway 175, 660 m, *Croat 39741* (MO); 8 km SW of Valle Nacional, 400 m, *Hernández & Chacón 491* (INB, MO). **Tabasco**: Grutas de Ocona near Teapa, 20–100 m, *Davidse et al. 29509* (CM, MO); Teapa, cultivated, *Croat 59160* (MO); Mpio. Tacotalpa, 0.2 km NW of Tapijulapa, *Cowan et al. 3496* (CSAT, MO). **Veracruz**: Valle de Córdova, *Bourgeau s.n.* (P); Route 185, 4 km NE of Minatitlan, 50 m, *King 1113* (MICH); 6 mi. E of Coatzacoalcos, 10 m, *Croat 40058* (MO); 7 km NE of Sontecomapan, 0–50 m, 18°33′30″N, 94°59′W, *Nee 22607* (F, MO); 5 km NW of Pajapan, Cerro San Martín, 750–900 m, 18°17′20″N, 94°43′W, *Nee & Calzada 22697* (F, MO, NY); Los Tuxtlas, 200 m, 18°42′N, 95°10′W, *Croat 63163* (MICH, MO, US). NICARAGUA. 40–45 km SW of Waspam, 10–100 ft., *Seymour 3776* (MO). **Jinotega**: Río Bocay, Salto Acatulu, ca. 130 m, 14°13′N, 85°10′W, *Stevens et al. 16750* (MO). **Matagalpa**: Comarca Wanawás, Río Bilampí, 180–200 m, 12°03–02′N, 85°13′W, *Araquistain & Moreno 2401* (MO, SAR); Cerro Musún, path to Palán, 300–600 m, *Araquistain & Moreno 2471* (AAU, LE, MO); 20 km E of Matagalpa, along Río Yasica, 700 m, *Neill 1963* (MO); Cerro Musún, 500–800 m, *Araquistain & Moreno 2571* (MO); Cerro Musún, 8 km from village of Wanawás, 500–800 m, 12°59–13°N, 85°14′W, *Araquistain & Moreno 2359* (MO); Quebrada Negra, Rio Bilampí, 500 m, *Neill 1816* (MO, US). **Río San Juan**: Bocas de Sábalo, 70–100 m, 11°03′N, 84°27′W, *Moreno 26748* (MO); above Río Sábalo, 40 m, 11°03′N, 84°28′W, *Moreno & Robleto 26016* (MO). **Zelaya**: ca. 14.3 km N of El Empalme, *Stevens 8303* (BM, MO); El Empalme–Rosita, along new road to Mina Nueva América, *Stevens 12667* (MO); *12668* (MO); *Pipoly 5293* (MO); 15 km W of Rama, 100 ft., *Harmon & Fuentes 5079* (MO); Kuikuinita, S of Siuna, 160 m, *Neill 4132* (MO); Río Prinzapolka–Quebrada San Rafael, Waní, ca. 100 m, 13°42′N, 84°50′W, *Pipoly 4578* (MO); *4587* (MO); *4588* (MO); *4589* (MO); Waní–Siuna, near Río Matías, ca. 0–100 m, 13°43′N, 84°49′W, *Pipoly 4682* (MO); *4701* (MO); Colonia Yolania–Colonia Manantiales (Colonia Somoza), ca. 200–300 m, ca. 11°36–37′N, 84°22′W, *Stevens 4825* (MO); Rosita–Puerto Cabezas, ca. 15.7 km SW of Río Kukalaya, <100 m, 13°58′N, 84°12′W, *Stevens 8502* (MO); Caño Zamora on Río Rama, ca. 10 m, ca. 11°57′N, 84°16′W, *Stevens 8821* (MO); Bonanza–Constancia, 160–360 m, ca. 13°58′–14°01′N, 84°37–40′W, *Stevens 12482* (MO); *12455* (MO); El Empalme–Limbaika, ca. 3.9 km SE, ca. 65 m, 13°39′N, 84°24′W, *Stevens 12883* (MO); *12886* (MO); vic. of Bonanza, 200–350 m, 14°01′N, 84°35′W, *Stevens 13031* (MO); *13053* (MO); 250–350 m, ca. 14°02′N, 84°34–35′W, *18786* (MO); 7.4 m SE, ca. 130 m, 13°38′N, 84°23′W, *21752* (MEXU, MO); *12346* (MO); ca. 140 m, ca. 14°01′N, 84°34′W, *Stevens 8056* (BM, MO); 1 km N of "Las Mercedes" settlement, 160–180 m, *Vincelli 334A* (MO); "Bodega" region, 30 km NE of Río Blanco, 80–100 m, 13°03′N, 84°58′W, *Moreno 24078* (MO); "San Agustín," SE of Rama, ca. 60 m, 12°09′N, 84°12′W, *Robleto 564* (MO); *Neill 3632* (MO); Bonanza–El Salto Grande, Laguna Santa Rosita, ca. 140–160 m, 14°03′N, 84°37′W, *Pipoly 3687* (MO); Mpio. Siuna, La Pimienta, *Ortiz 1966* (MO); Río Mico, Experimental Station El Recreo, 30 m, 12°10′N, 84°18′W, *Davidse et al. 30768* (MO); Río Prinzapolka, ca. 2 km S of Waní, ca. 0–100 m, 13°42′N, 84°50′W, *Pipoly 4733* (MO), *4738* (MO), *4747* (MO); Río Punta Gorda, Atlanta, 10 m, 11°34′N, 84°01′W, *Moreno & Sandino 12769* (MO); Waspam–Puerto Cabezas, Río Troncera, <200 m, ca. 14°43′N, 84°06′W, *Pipoly 4042* (MO); Río Wilike Grande, Wilike region, 100 m, 13°05′N, 84°57′W, *Moreno 23999* (MO). PANAMA. **Bocas del Toro**: Fortuna Dam–Chiriquí Grande, 3.2 mi. N of Continental Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60281* (MO); Changuinola–Almirante, Milla 7.5, *Croat & Porter 16241* (MO); Valle del Silencio, Río Changuinola, ca. 1 km above mouth of Río Teribe, <100 m, 9°21′40″N, 82°31′40″W, *Croat & Zhu 76431* (MO). **Canal Area**: Frijoles, 25–30 m, *Pittier 3755* (US); Barro Colorado Island, *Shattuck 182* (F, GH, MO); *Ebinger 99* (MO); *Croat 11838* (MO); *Schmalzel 797* (MO); *Dwyer et al. 8474* (MO); *Croat 16535* (MO); *15067* (MO); *11006* (MO); *10741* (MO, UC); *10198* (MO, SCZ); *10085* (MO); *6214* (MO); *6294* (MO); *8605* (MO); *8040* (MO); *6861* (MO); *6495* (MO); *4001* (MO); Summit Garden, *Croat 17058* (MO); *10284* (MO, SCZ); *33015* (MO); *10915* (MO). **Chiriquí**: Volcán–Serrano, 7 mi. N of Volcán, 8°50′N, 82°38′W, *Croat 66228* (MO); vic. El Hato del Volcán at Las Lagunas, 3 mi. from Nueva California, 1380 m, 8°46′N, 82°40′W, *Croat 67707* (MO, PMA); vic. Santa Clara, 1520 m, *Croat 66288* (F, MO); Gualaca–Chiriquí Grande 2.5 mi. beyond Los Planes de Hornito, 1099 m, 8°40′N, 82°13′W, *Croat 67739* (CM, MO); 2.8 mi. beyond Los Planes, 1200 m, *48817* (MO); Quebrada La Mina, 2.3 mi. N of Los Planes, 800 m, 8°41′N, 82°13′W, *Croat & Zhu 76364* (CM, MO); along Río Colorado, 1200–1400 m, 82°43′W, 8°50′N, *Hamilton & Krager 3757* (MO, RSA); vic. Boquete, ca. 1450 m, *Croat 26744* (MO). **Coclé**: La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, *Croat 67210* (CM, MO); *Croat 13358* (MO); ca. 1 mi. N of El Valle, *Gentry & Dwyer 3591* (MO); 900 m, *Gentry 7433* (F, GH, MO). **Coclé–Panamá**: trail beyond La Mesa towards Los Llano and the border, *Luteyn 3178* (MO); 850–900 m, *Luteyn 4066* (MO). **Colón**: Santa Rita Ridge, 26 km from Transisthmian Highway, 500 m, 9°26′N, 79°57′W, *Knapp et al. 1708* (MO); Mile ca. 12, ca. 500 m, 9°25′N, 79°40′W, *McPherson 11760* (MO). **Darién**: Parque Nacional del Darién, ca. 17 km E of Pucuro, Río Pucuro, 750–850 m, 8°03.5′N, 77°17′W, *Hammel et al. 16293* (MO); western slopes of Cerro Pirre, 17 km N of El Real, Río Perisenico, 100 m, 8°01′N, 77°40W, *Croat & Zhu 77187* (MO); vic. Cana, 500–600 m, *Croat 37641* (MO); Alturas de Nique region, 900–1250 m, 7°45′N, 77°40′W, *McPherson 11603* (MO); Cerro Sapo, 800 ft., *Hammel 1330* (MO); E base of Cerro Sapo along stream (Río Celorio?), 1300 ft., *1131* (MO); 18 km SE of Jaque, 25 m, *Garwood et al. 98* (BM, CM, MO, PMA); N of Punta Guayabo Grande, NW of Ensenada El Guayabo ridges, 0–200 m, 7°24′N, 78°07′W, *Knapp & Mallet 3160* (MO, US); Río Coasi, Cerro Coasi, *Duke 15554* (US); Río Cocalito, SE of Jacque, 7°18′N, 77°58′W, *Whitefoord & Eddy 223* (BM, MEXU, MO). **Panamá**: Juan Díaz, *Standley 30618* (US); Cerro Jefe region, 750–800 m, 9°14′N, 79°22′W, *Croat 67082* (F, MO); *67084* (MO); 4.6 km beyond peak on road to Altos de Pacora, ca. 600 m, *Croat 35900* (MO); at Altos de Pacora, 750 m, 9°15′N, 79°29′W, *Croat & Zhu 76606* (MO); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68636* (CM, MO); Campo Tres, 5 km NE of Altos de Pacora, *Busey 835* (MO); Lago Cerro Azul, 500 m, *Sullivan 82* (MO); Cerro Campana, 2500 ft., *Hammel 3767* (MO, SEL); Río Majé–Quebrada Brava, 60 m, *Croat 34630* (MO); El Llano–Cartí Road, 7–12 km from

Interamerican Highway, 360–400 m, *Croat 25122* (MO); Km ca. 16–18, 400 m, *Tyson & Nee 7355* (MO); El Llano Cartí road, Mile 10.6, ca. 400 m, 9°17′N, 78°58′W, *Miller et al. 862* (MO); Mile 6–10, 200–250 m, 9°15–16′N, 78°59′W, *Thompson 4704* (CM, MO); Serranía de Majé, along Río Ipetí, near confluence with Río Ambrosio, 100 m, 8°57′N, 79°32′W, *Churchill & de Nevers 4480* (MO, PMA, RSA). **San Blas**: Nusagandi, along El Llano–Carti Road, 11.6 mi. N of highway, 450 m, 9°18′N, 79°59′W, *Croat 75135* (CM, MO, PMA). **Veraguas**: Santa Fe–Río San Luis, vic. Río Tercero Brazo, 700 m, 8°33′N, 81°08′W, *Croat 66925* (MO, PMA); Río Dos Bocas, ca. 5–8 km N of Alto Piedra, 730–770 m, *Croat 25915* (MO); ca. 500 m, *Croat 34242* (MO); vic. Escuela Agrícola–Calovébora, ca. 1200 m, 81°07′W, 8°32′N, *Hamilton et al. 1279* (MO).

Philodendron tysonii Croat, sp. nov. TYPE: Panama. Chiriquí: Gualaca–Chiriquí Grande, 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *Croat 67844* (holotype, MO–3614677; isotypes, AAU, B, CAS, CM, CR, DUKE, F, GH, K, M, MEXU, NY, P, PMA, RSA, US, VEN, W). Figures 29, 425–430.

Planta plerumque hemiepiphytica, interdum terrestris; internodia 2–6 cm longa, 3.5–4 cm diam.; cataphylla (10)21–33 cm longa, incostata vel leniter 1-costata, saepe rubella, persistentia semi-intacta, demum decidua; petiolus teres vel subteres, 39–90 cm longus, 8–15 mm diam.; lamina ovata, coriacea, nitida, 32–70 cm longa, 24–50 cm lata; costa postica plerumque vix aut haud nuda, raro nuda 3 cm; inflorescentia 4–5; pedunculus 3–12 cm longus, 3–8(11) mm diam.; spatha 11.5–19 cm longa, lamina spathae extus viridi, suffusa marronina aut rubella, intus alba vel pallide viridi; tubo spathae extus suffuso marronino aut rubello, intus atrimarronina suffuso in laminam; pistilla (5)6–8(9)-locularia; loculi (4)5–7-ovulati.

Usually hemiepiphytic, appressed-climber, sometimes terrestrial; internodes short, stout, semiglossy, smooth, 2–6 cm long, 3.5–4 cm diam., dark green; roots elongate, fine, branched; cataphylls (10)21–33 cm long, unribbed to weakly 1-ribbed, sometimes sharply 2-ribbed near base and unribbed near apex, frequently reddish, frequently striate, emarginate at apex, persisting semi-intact at upper nodes, eventually deciduous, emarginate at apex; **petioles** 39–90 cm long, 8–15 mm diam., terete to subterete, surface densely pale-striate, glossy; sheath 10.5–11 cm long; **blades** ovate, coriaceous to moderately coriaceous, glossy to semiglossy, conspicuously bicolorous, acuminate at apex (the acumen sometimes inrolled and twisted), cordate at base, 32–70 cm long, 24–50 cm wide (1–1.8 times longer than wide and averaging 1.4 times), (0.4–1.1 times longer than petiole), averaging about ¾ as long as petiole, upper surface dark green, drying dark brown to blackish brown, lower surface slightly paler, drying dark yellow-brown to greenish brown; anterior lobe 25–52.5 cm long, 20–50 cm wide (2–4.8 times longer than than posterior lobes); posterior lobes broadly rounded to broadly obtuse, 8–20 cm long, 11–22 cm wide; sinus parabolic, sometimes spatulate, (3)4–12 cm deep; midrib broadly convex to almost flat, conspicuously paler than surface above, convex to bluntly acute, darker than surface below; basal veins 5–9 per side, with (0)1(2) free to base, numbers 3–4 coalesced 1.5–3 cm; posterior rib usually scarcely or not at all naked, rarely naked for 3 cm; primary lateral veins 4–10 per side, departing midrib at a 60–70° angle, moderately straight to the margins, narrowly sunken above, convex and somewhat paler than surface below; interprimary veins sunken, usually concolorous above, raised, darker than surface below; minor veins moderately distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES 4–5 per axil; peduncle 3–12 cm long, 3–8(11) mm diam., green, finely striate; **spathe** 11.5–19 cm long (1.5–4.5 times longer than peduncle); spathe blade green to white, lightly to heavily tinged maroon or reddish, finely striate-speckled, margins clear outside, white to pale green inside; spathe tube tinged maroon or reddish, finely striate-speckled outside, 4.5–10 cm long, dark maroon, suffused into blade inside, weakly constricted above the tube; **spadix** white throughout, 10.7–15.6 cm long; pistillate portion 3.4–5.2 cm long in front, 2.4–3.1 cm long in back, broadest midway and gradually tapered toward both ends, 1.2 cm diam. at apex, 1.2–1.4 cm diam. at middle; staminate portion 7.7–9.4 cm long; fertile staminate portion white, barely constricted above the sterile staminate portion, barely tapered toward apex, 1–1.2 cm diam. at base, 1–1.2 cm diam. at middle, 6–7 mm diam. ca. 1 cm from apex; sterile staminate portion 9–10 mm diam.; pistils 1.5–2.7 mm long, 0.8–1.6 mm diam., white; ovary (5)6–8(9)-locular, with sub-basal placentation; locules (0.8)1.1–1.3 mm long, 0.3–0.6 mm diam.; ovules (4)5–7 per locule, (0.1)0.3–0.4 mm long, 2-seriate, contained within transparent ovule sac; style similar to style type B; stigma 0.8–1.2 mm diam., 0.2–0.3 mm high. INFRUCTESCENCE with pistillate spadix 6.5 cm long, 4 cm diam.

Flowering in *Philodendron tysonii* occurs mostly in June and July but also in September. In reality, flowering probably occurs from January through September or perhaps October, since post-anthesis collections have been made nearly throughout the year except February. Immature fruiting collections have been made in March, September, and November.

Philodendron tysonii is known only from Panama, but is expected to be found in the Cordillera

de Talamanca of Costa Rica. It ranges from 600 to 1500 m elevation in *Premontane rain forest* and *Tropical Lower Montane rain forest* life zones.

Philodendron tysonii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Reticulata.* This species is characterized by its stout, short (usually 3–5 cm diam.) internodes; unribbed or weakly one-ribbed, frequently reddish cataphylls persisting semi-intact (often becoming fibrous) at the upper nodes; terete to subterete petioles; and ovate-cordate blades averaging 1.4 times longer than wide and about three-fourths as long as the petioles, with 6–9 basal veins and a weakly developed posterior rib, which is rarely naked at the sinus.

Philodendron tysonii is perhaps most easily confused with *P. antonioanum,* with which it may occur. The latter species differs in having sharply 2-ribbed cataphylls, blades drying gray-green with prominulous "cross-veins" and 4 to 6 pairs of primary lateral veins, and short-pedunculate inflorescences with spathe tubes dark magenta on both surfaces and barely constricted above. In contrast, *P. tysonii* has usually bluntly 1-ribbed cataphylls, blades drying ± blackened and smooth above, 6–10 primary lateral veins, more prominently pedunculate inflorescences, and prominently constricted spathes merely tinged red on the tube outside. In addition, the two species differ in the nature of their ovules, with *P. tysonii* having (5)6–8(9)-locular ovaries with (4)5–7 ovules per locule borne in an envelope with sub-basal placentation, while *P. antonioanum* has 5-locular ovaries with about 30 ovules per locule, with parietal placentation and not borne in an envelope.

This species may also be confused with *P. sagittifolium* (especially broader-leaved forms), which shares blades with mostly free basal veins with posterior ribs short or lacking and scarcely or not at all naked along the sinus. The latter species differs in having narrower stems (rarely more than 3 cm diam.), green, sharply 2-ribbed deciduous cataphylls (vs. persistent in *P. tysonii*), and blades usually somewhat reddish brown and proportionately longer (averaging about 2 times longer than broad) with the posterior lobes usually narrowly rounded. In addition, the juvenile blades of *P. sagittifolium* are elongated, usually oblong to narrowly triangular, and usually up to 2.5 times longer than wide (vs. ovate to narrowly ovate, less than 2.5 times longer than wide, and with broadly rounded posterior lobes in *P. tysonii*).

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, just N of the Continental Divide, 850–950 m, 8°46′N, 82°17′W, *Hammel et al. 14700* (MO); ca. 8.5 mi. from bridge over Fortuna Lake, 600 m, 8°46′N, 82°16′W, *Croat 67005* (CAS, CM, L, MO, PMA, TEX); Cerro Colorado, 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69017* (DUKE, IBE, MEXU, MO, NY, PMA, QCA, RSA, WIS); 7 mi. from Chame, ca. 1500 m, 8°35′N, 81°45′W, *McPherson 8810* (MO); 5.3 mi. N of center of Fortuna Dam, Continental Divide Trail, 8°44′N, 82°17′W, *Croat & Zhu 76346* (MO); near Lago Fortuna, along trail to Río Hornito, 8°45′N, 82°18′W, *Croat & Zhu 76374* (MO, PMA). **Chiriquí**: Cerro Colorado, above San Félix, 18–27 mi. N of Pan-American Highway, 1200–1500 m, *Croat 33148* (MO); 24 mi. N of Río San Félix, 1430–1500 m, *48486* (MO); 34.1 km N of Río San Félix, 1390 m, *37258* (MO); 28 mi. above Río San Félix, 1200–1500 m, *33269* (MO); from Chame to ca. 9 mi. along road, 1100–1750 m, 8°35′N, 81°54′W, *Hammel & Trainer 15008* (MO, NY); Fortuna Dam area, Fortuna–Chiriquí Grande, Continental Divide, 1170 m, 8°44′N, 81°17′W, *Croat 66711* (B, BR, COL, CR, K, MO, NY, PMA, US); *Hammel & Kress 13490* (DUKE); Continental Divide trail, 8°44′N, 82°17′W, *Croat & Zhu 76330* (K, MO, NY, SCZ, US); trail to Río Hornito, 1100–1350 m, 8°45′N, 82°15′W, *McPherson 11660* (MO); *Croat & Zhu 76417* (AAU, CM, ENCB, GB, IBE, M, MO, NY, PMA, TEX, WIS); confluence of Río Hornito and Río Chiriquí, 1050–1100 m, ca. 8°44′N, 82°13′W, *Stevens 18376* (MO); *18377* (MO); vic. IRHE facilities, 1100–1200 m, 8°45′N, 82°08′W, *Croat 66589* (AAU, COL, DUKE, F, K, MBM, MEXU, MO, P, PMA, US, VDB); 1300 m, *Croat 48760* (CM, MO); Quebrada Los Chorros–Quebrada Frank, N of reservoir, 1100 m, 8°45′N, 82°13′W, *Churchill & Churchill 6081* (MO); 8.3 mi. beyond Los Planes de Hornito, 1260 m, 8°44′N, 82°16′W, *Croat 49943* (MO); 1300 m, 8°45′N, 82°17′W, *49821* (MO); 1400 m, *48704* (AAU, MEXU, MO, U, UC, W). **Coclé**: El Copé region, Alto Calvario, Continental Divide, 9.4 km above El Copé, 750–900 m, *Croat 44719* (MO); 710–800 m, 8°39′N, 80°36′W, *68766* (MO, PMA); 850 m, *67577* (AAU, CM, F, G, L, MEXU, MO, NY, PMA, TEX, US); 930 m, *49203* (MO); 650–850 m, *Folsom 6217* (MO). **Panamá**: Cerro Jefe region, vic. of summit, 9°15′N, 79°30′W, *Croat & Zhu 76210* (CM, MO); *Witherspoon & Witherspoon 8531* (MO); ca. 1000 m, *Croat 49084* (CAS, K, MO, PMA); 1000 m, 9°15′N, 79°30′W, *Knapp 2240* (MO); La Eneida, 1000 m, *Luteyn & Kennedy 1775* (DUKE); 0.8 mi. beyond turnoff to Altos de Pacora, 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76614* (CM, MO, WIS); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68688* (AAU, CM, F, G, MEXU, MO, PMA, TEX, US); 800–1000 m, *22671* (F, MO); 2400 ft., *Antonio 4753* (MO); *Croat 67059* (AAU, B, BR, C, CAS, CM, COL, CR, DUKE, EAP, ENCB, F, HNMN, HUA, IBE, JAUM, JBGP, K, L, M, MO, NY, PMA, QCA, US, USCG, WIS); 850–900 m, 9°15′N, 79°30′W, *McDonagh et al. 36* (BM); ca. 1000 m, *Mori et al. 3737* (MO); ca. 950 m, ca. 9°15′N, 79°30′W, *McPherson 7109* (MO); Cerro Azul–Cerro Jefe, ca. 1000 m, *Luteyn 3209* (DUKE); 3000 ft., *Tyson et al. 4449A* (MO, SCZ); Campo Tres, ca. 700 m, *Croat 27047* (F, L, MO, US); El Llano–Cartí, 6.8 mi. from highway, 350 m, *Croat 49120* (MO). **Veraguas**: Santa Fe region, Alto Piedra–Calorébora, 3200–5600 ft., *Hammel 4604* (MO); Río Tercero Brazo, beyond Alto Piedra, *Croat 27328* (MO); between Río Tercero Brazo and summit of hill leading down to the Atlantic lowlands, 700 m, 8°33′N, 81°08′W, *Croat 66926* (B, CAS, F, K, MO, PMA, US); Parque Nacional Cerro Tute, near Alto Piedra,

0.5 mi. N of Alto Piedra, 1250–1350 m, *Croat 48955* (F, MO); 800–1030 m, *Croat & Zhu 76911* (CM, MO).

Philodendron ubigantupense Croat, sp. nov. TYPE: Panama. San Blas: on mainland opposite Isla Miria Ubigantupo, along trail to Digole, to 20 m, 9°26′N, 78°54′W, 19 July 1987, *H. Herrera 294* (holotype, MO–3585503; isotype, PMA). Figure 436.

Planta hemiepiphytica; internodia usque to 7.5 cm longa, 1 cm diam.; cataphylla decidua; petiolus subteres, 12–13 cm longus, in sicco 5–6 mm diam.; lamina oblonga, anguste cordulata basi, 27–32 cm longa, 8.5–9 cm lata, in sicco caniviridis; nervis lateralibus I obscuris; inflorescentia 1; pedunculus 8 cm longus, in sicco 5 mm diam.; spatha 9.3 cm longa, viridis; pistilla (7)8-locularia; loculi 1-ovulati.

Hemiepiphytic; stem scandent; internodes to 7.5 cm long, 1 cm diam., slender, drying 7 mm diam., gray-brown, irregularly and closely fissured, somewhat flaking; roots several per node, drying moderately smooth, reddish brown, semiglossy; cataphylls lanceolate, deciduous; **petioles** 12–13 cm long, drying 5–6 mm diam., subterete, drying dark gray-brown, minutely striate, sheathed to 1.5 cm; **blades** oblong, acuminate at apex (the acumen tightly inrolled, 5 mm long), narrowly cordulate at base, 27–32 cm long, 8.5–9 cm wide (3–3.8 times longer than wide), (2.2–2.5 times longer than petiole), about as long as petiole; upper surface dark green, drying weakly glossy, gray-green, lower surface slightly paler, semiglossy, drying greenish gray; sinus to 1.3 cm deep; midrib broadly convex above, convex and paler below, drying faintly striate; primary lateral veins almost totally obscure above and below; many minor veins, all free to base, arising from the midrib only, drying obscure above, close and weakly raised below, spreading at a 55–75° angle, ± straight to the margin. INFLORESCENCES solitary; peduncle 8 cm long, drying 5 mm diam.; **spathe** green, 9.3 cm long, (1.2 times longer than peduncle); spathe tube weakly constricted, ca. 4.5 cm long; **spadix** bluntly pointed at apex, 10.8 cm long; pistillate portion 4 cm long in front, 3.7 cm long in back, 8 mm diam. at apex, drying 1 cm diam. at middle; staminate portion 8.1 cm long; fertile staminate portion 8.5 mm diam. at middle, 6.5 mm diam. ca. 1 cm from apex; sterile staminate portion 8 mm diam. at apex, 9 mm diam. at base; pistils 1.5 mm long; ovary (7)8-locular, 1.2 mm diam., with sub-basal placentation; locules 1.1 mm long, 0.2–0.3 mm diam.; ovule sac ca. 1 mm long; ovules 1 per locule, contained within transparent ovule sac, ca. 0.3 mm long; funicle ca. 0.3 mm long (can be pulled free to base), style 0.9 mm diam., similar to style type D; style apex sloping to weakly rounded; style boss moderately broad and fairly pronounced; the androecium truncate, sometimes prismatic and weakly clavate, margins irregularly 4–5-sided, 0.8–1.5 mm long; thecae oblong, 0.2–0.3 mm wide, ± parallel to one another; sterile staminate flowers clavate to prismatic, irregularly 4–5-sided, 1.3–1.7 mm long.

The flowering phenology of *Philodendron ubigantupense* is uncertain owing to its rarity, but since it has small inflorescences and was in flower in July, it probably both flowers and fruits in the wet season.

Philodendron ubigantupense is endemic to Panama, known only from the type locality along the Atlantic coast, at or near sea level in a *Premontane wet forest* life zone.

Philodendron ubigantupense is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is characterized by its scandent habit, long, slender internodes, subterete petioles and especially by its oblong, gray-green drying blades over twice as long as the petioles, weakly cordulate leaf bases, and almost totally obscure primary lateral veins.

Philodendron ubigantupense is perhaps most similar to *P. folsomii,* which has blades of similar size and color. The latter species differs in having short internodes and blades merely rounded at the base and with 8–10 distinct primary lateral veins. In addition, *P. folsomii* has 6–7 locules per ovary, whereas *P. ubigantupense* has mostly 8 locules per ovary. *Philodendron immixtum* is another species that might be confused with *P. ubigantupense,* but it differs in having proportionately broader blades (to 2.8 times longer than broad) with up to five, obvious primary lateral veins.

Philodendron utleyanum, Croat, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge, about 7 mi. from Transisthmian Highway, ca. 200 m, 21 Dec. 1971, *Wilbur et al. 15068* (holotype, DUKE 226389). Figures 431, 432.

Planta hemiepiphytica; internodia 1–3.5 cm longa, 1.5–2 cm diam., in sicco pallide brunnea; cataphylla usque 27 cm longa, leniter 2-costata, in sicco obscure rubribrunnea, decidua; petiolus subteres, atribrunneus, obtuse subcomplanatus adaxialiter versus apicem, 19–21.5 cm longus, in sicco 6–7 cm diam.; lamina oblongo-oblanceolata, 32–39 cm longa, 10–14 cm lata, aliquantum inequilaterala et rotundata vel truncata aut leniter cordulata basi, atriviridis supra, in sicco canobrunnea, saepe aliquantum rubella infra, in sicco brunnea; nervis basalibus 2–3 utroque, omnibus liberis ad basim; inflorescentia 1; pedunculus usque 9 cm longus, in sicco atribrunneus; spatha usque 11 cm longa, pallide viridis, extus suffusa

subrosea, intus alba, tubo spathae 5 cm longa; pistilla 4–5-locularia; loculi 1-ovulati.

Hemiepiphytic; stem appressed-climbing; internodes drying moderately glossy, irregularly and acutely ribbed with a few flat smooth intervening areas, 1–3.5 cm long, 1.5–2 cm diam., drying light brown; roots several per node, short, drying brown, to 3 cm diam.; cataphylls to 27 cm long, weakly 2-ribbed, but sharply 2-ribbed toward the apex, red tinged toward the base, drying dull reddish brown, deciduous; **petioles** 19–21.5 cm long, drying 6–7 cm diam., subterete, dark brown, obtusely somewhat flattened toward the apex adaxially, surface smooth to weakly ribbed; **blades** somewhat inequilateral, oblong-oblanceolate, subcoriaceous, semiglossy, acuminate at apex, somewhat inequilateral and rounded to truncate to weakly cordulate at base, 32–39 cm long, 10–14 cm wide, broadest above the middle, 1.3–1.8 times longer than petioles, upper surface dark green, drying gray-brown, lower surface often somewhat reddish, drying medium brown; posterior lobes to ca. 2 cm long; midrib drying weakly and obtusely raised, slightly paler than surface above, drying convex, drying light brown with a distinct pale border along its edges and paler than surface below; basal veins 2–3 per side, and with all free to base; primary lateral veins 8–9 per side, departing midrib at a 65–80° angle in the lower one-half, to 45° angle toward apex, weakly arcuate to the margins, drying inconspicuous except near the midrib, paler than surface above, weakly convex and paler than surface, sometimes undulate below; minor veins drying moderately inconspicuous and close, weakly undulate, arising from the midrib only, the surface and minor veins minutely and densely granular at 10× magnification. INFLORESCENCES 1 per axil; peduncle to 9 cm long, drying 4.5 mm diam., dark brown; **spathe** moderately coriaceous, to 11 cm long, ca. 2 cm diam., pale green with pinkish tinge, drying dark brown throughout, white within; spathe tube 5 cm long, 1.8–2 cm diam.; **spadix** sessile, 10 cm long.; pistillate portion 5 cm long, drying to 1.7 cm diam. near base, 1.5 cm diam. midway, 1 cm at apex; staminate portion 4.7 cm long, too deteriorated for detailed studies; pistils 2.5–3 mm long, 1.5–2 mm diam., drying light brown, smooth except warty near apex; style type not studied; stigma 0.4–0.6 m diam., button-like on drying with a medial nipple and 4–5 radiate arms, sometimes with fragments of the dried stigma apron-like still attached; locules 4–5; ovaries with sub-basal placentation, 1 ovule per locule.

Flowering in *Philodendron utleyanum* is poorly known. The single collection with immature fruits was made in December. This species probably flowers in the rainy season.

Philodendron utleyanum is endemic to Panama, known only by the type specimen from Colón Province in a region of *Premontane wet forest* at 200 m elevation.

Philodendron utleyanum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is distinguished by its short tan internodes; sharply 2-ribbed, deciduous cataphylls; subterete petioles about three-fourths as long as the blades; and oblong-oblanceolate, brown-drying blades broadest above the middle and rounded to weakly subcordate at the base.

In terms of coloration and texture, *P. utleyanum* appears closest to *P. sagittifolium,* but in terms of blade shape it is closest to *P. pseudauriculatum.* The former differs in having the blades broadest at the base and decidedly cordate, the latter in having dark gray-green-drying leaves, more or less spongy, proportionately shorter petioles, and the spadix clearly demarcated from the peduncles by a marked color contrast. *Philodendron utleyanum* lacks any clear limit between the peduncle and the spathe.

This species is named in honor of John Utley, a participant in the Duke University expedition that collected the type. Utley has been responsible for collecting many interesting and important Araceae during his trips to Central America and during his tenure as a Peace Corps volunteer in Costa Rica.

Philodendron verapazense Croat, sp. nov. TYPE: Guatemala. Alta Verapaz: 7 mi. on road to Oxec, along road turning N off Hwy. 7E between Tucurú and El Estor, ca. 6 km NE of Panzós, 700 m, ca. 15°28′N, 89°04′W, *Croat 41656* (holotype, MO–2743518; isotypes, GUAT, US). Figures 433–435.

Planta hemiepiphytica; internodia longiora quam lata, conspicue multisulcata; cataphylla 14–17 cm longa, acute 2-costata, decidua; petiolus acute D-formatus complanatus adaxialiter, 29–44 longus, in sicco 2–5 mm diam.; lamina anguste ovato-triangulari-cordata, longe acuminata apice, longe cordata vel sagittata basi, 26–34 cm longa, 11.5–14 cm lata; nervis lateralibus I 3–4 utroque; inflorescentia 1; pedunculus 3–14 cm longus, 4–5 mm diam.; spatha 10–18 cm longa, extus rubriviolacea; tubo spathae intus carmesino; pistilla 4–6-loculari; loculi 2-ovulati.

Hemiepiphytic; stem appressed-climbing or sometimes scandent; pre-adult internodes to 20 cm long, 1.5–3 cm long; adult internodes green becoming tinged purple, finally tan, conspicuously many-sulcate except above each petiole, longer than broad; roots few per node, 10–30 cm long,

drying dark brown, weakly glossy, 2.3 mm diam.; cataphylls 14–17 cm long, sharply 2-ribbed, green tinged red, deciduous; **petioles** 29–44 cm long, drying 2–5 mm diam., sharply D-shaped, flattened adaxially, with adaxial margins sharp; **blades** narrowly ovate-triangular-cordate, subcoriaceous, long-acuminate at apex (the acumen sometimes apiculate), long-cordate to sagittate at base, 26–34 cm long, 11.5–14 cm wide (2–3 times longer than wide), (0.7–1.1 times longer than petiole); anterior lobe (13)21–26 cm long, (5.4)13–14 cm wide (2.9–4.3 times longer than posterior lobes); posterior lobes 6–7.5 cm long, (2.3)6–7.1 cm wide; sinus hippocrepiform, sometimes spathulate, 7–7.5 cm deep; midrib broadly convex and paler above, convex and darker below, drying somewhat acute; basal veins 3(4) per side, with 0(1) free to base, the remainder coalesced 2–2.5 cm; posterior rib naked for most or all of its length; primary lateral veins 3–4 per side, departing midrib at a 55–65° angle, ± straight to weakly arcuate to the margins; minor veins arising from the midrib only. INFLORESCENCES 1 per axil; peduncle 3–14 cm long, 4–5 mm diam., green or tinged with reddish violet; **spathe** 10–18 cm long ((0.7)2–3.7 times longer than peduncle), reddish violet outside; spathe blade acuminate; spathe tube cylindrical, 8–9 cm long, 1–1.5 cm diam., crimson-red inside; **spadix** stipitate to 3.5 cm long; acute at apex, 15–16.5 cm long, constricted ca. 4 cm above base of sterile staminate portion; pistillate portion cream, 3.2 cm long in front, 1.7 cm long in back, 1.5–2.6 cm wide at base; staminate portion 8.3–9 cm long; fertile staminate portion cream, tapered to apex, 7–10 mm diam. at base and midway, 3–4 mm diam. ca. 1 cm from apex; sterile staminate portion 1.8–2.2 mm diam.; pistils 1.9–2.3 mm long; ovary 4–6-locular, 1 mm diam., with sub-basal placentation; locules 0.9 mm long, ca. 0.3 mm diam.; ovule sac 0.4–1 mm long; ovules 2 per locule, contained within transparent, gelatinous ovule sac, longer than funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style 0.8 mm diam., similar to style type D; style apex somewhat rounded to flat, depressions surrounding stylar canal exits, style boss broad, very shallow; the androecium truncate, prismatic, ± oblong, margins irregularly 5–6-sided, 0.8–1.1 mm long; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another, very nearly contiguous; sterile staminate flowers prismatic to weakly clavate, irregularly 4–6-sided, mostly 5-sided, 1.3–1.9 mm long.

Flowering in *Philodendron verapazense* occurs in April and May, with a single, post-anthesis collection known from July.

Philodendron verapazense ranges from southern Mexico (Chiapas) to Guatemala (Alta Verapaz), at 700 to 1525 m elevation in "Bosque Pino-Encino" in Mexico and *Tropical moist forest* in Guatemala.

Philodendron verapazense is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium.* This species is recognized by its scandent habit with the internodes longer than broad and conspicuously pluri-sulcate, as well as by its sharply two-ribbed, deciduous cataphylls, sharply D-shaped petioles, narrowly ovate-triangular-cordate blades, solitary inflorescences, red to reddish violet spathe tubes, and greenish spathe blades.

Philodendron verapazense is probably most similar to *P. sagittifolium* especially in the shape and coloration of the blades, the sharply two-ribbed, deciduous cataphylls, and the D-shaped petioles. It differs from the latter species principally in its deeply sulcate stems, sharply D-shaped, shorter (less than 50 cm long) petioles, and leaf blades with 3–4 pairs of primary lateral veins (vs. subterete, longer petioles, which are greater than 50 cm long, and 4–8 pairs of primary lateral veins for *P. sagittifolium*).

Additional specimens examined. GUATEMALA. **Alta Verapaz**: near Chirriacté, on the Petén Highway, ca. 900 m, *Standley 91978* (F). **Izabal**: vic. EXMIBAL camp 2, NW of Lake Izabal, 400–500 m, *Jones & Facey 3354* (NY). MEXICO. **Chiapas**: Los Lagos, 3 mi. NW of Rancho San José, 5000 ft., *Carlson 1846* (F).

Philodendron verrucosum L. Mathieu ex Schott, Syn. Aroid. 85. 1856. TYPE: Locality unknown (holotype, W? lost?). Schott ic. 2757–2759 (neotype, here designated). Figures 437–440, 445.

Philodendron daguense Linden & André, Ill. Hort. 18: 192, t. 79. 1871. TYPE: Colombia. Valle: Río Dagua, *Wallis s.n.* (holotype, K).

Philodendron pilatonense Engl., Bot. Jahrb. Syst. 37: 129. 1905. TYPE: Ecuador. Pichincha: Río Pilatón, May 1899, *Sodiro s.n.* (holotype, B; isotypes, G, MO).

Philodendron discolor K. Krause, Notizbl. Bot. Gard. Berlin-Dahlem 9: 273. 1925. TYPE: Peru. Junín: Prov. Jauja, in the valley of Río Masamerich (Río Pontachuela) confluent of Río Pangoa, above Rasthütte Calabaza, 1500–1600 m, 11°30′S, 7 May 1913, *Weberbauer 6663* (holotype, B; isotype, F).

Usually hemiepiphytic, rarely terrestrial or epiphytic; stem appressed-climbing, densely scaly or setose, trichomes green to greenish white; pre-adult internodes to 20 cm long, 1–2 cm diam.; adult internodes smooth, scurfy, minutely wrinkled, semiglossy to matte, 3–10 cm long, 2–6 cm diam., about as long as broad or longer than broad, gray to brown, roots moderately numerous, mostly short,

covered at least on one side with fine root hairs, drying dark brown, semiglossy, faintly appressed-scaly; cataphylls 10–30 cm long, unribbed, sometimes bluntly 1-ribbed, green or reddish, densely scaly or setose, persisting as a tangled network of fibers. LEAVES erect-spreading; **petioles** 33–65(90) cm long, 3 cm diam. at base, 1.5 cm diam. at apex, subterete, purplish violet to brownish, surface densely scaly, the scales of two distinct types, short, broad, often lacerate scales interspersed with long acicular scales, the latter erect, or spreading then erect; **blades** broadly ovate-cordate, thinly coriaceous, moderately bicolorous, acuminate to narrow acuminate at apex (the acumen mostly inrolled, 1–2.5 mm long), cordate at base, 28–75 cm long, 19–60 cm wide (1–1.7 times longer than wide), (0.7–1.5 times longer than petiole), broadest below point of petiole attachment, upper surface dark green or bronze-green (blackish green on new leaves), velvety to matte, drying dark brown, yellow-green or gray-green, lower surface pale green tinged red-purple between secondary veins (weakly glossy and purple-violet on new leaves), matte, drying yellow-brown to reddish brown; anterior lobe 9.6–51 cm long, 10–59 cm wide (1.9–3 times longer than posterior lobes); posterior lobes 8–21 cm long, 5–28 cm wide, broadly rounded to obtuse; sinus hippocrepiform to obovate or closed; midrib flat to sunken, slightly paler than surface above, convex, matte, darker than surface below; basal veins 6–8 per side, with (0)1–2 free to base, numbers 3–4 coalesced 1–5 cm; posterior rib not at all naked on small blades or naked for 0.5–6 cm; primary lateral veins 3–6(8) per side, departing midrib at a 50–55° angle, sunken, paler than surface above, round-raised to convex, darker than surface below; minor veins distinct and darker than surface below, arising from both the midrib and primary lateral veins; "cross-veins" conspicuous, in part raised below. INFLORESCENCES 1–4 per axil; peduncles 5–25 cm long, 1–2 cm diam., medium green to purplish, usually 0.66–1.75 times longer than the spathe; **spathe** densely scaly or setose, 10–22 cm long, 4 cm diam.; spathe blade medium green, whitish or reddish green outside, white to pinkish inside; spathe tube reddish green, medium green, or dull purple-violet outside, red or pale reddish (dark green post-anthesis) inside; **spadix** 14.6 cm long; pistillate portion cylindrical to weakly clavate, 1.8–4.6 cm long, 1 cm diam. at apex, 8 mm wide at base; staminate portion 9.4 cm long; fertile staminate portion cream; pistils 2.6–3.3 mm long, 1.4–1.7 mm diam.; ovary 4–5-locular, 1.9–2.5 mm long, 1.4–1.7 mm diam., with axile placentation; locules 1.9–2.5 mm long, 0.5–0.7 mm diam.; ovule sac 1.8–2.2 mm long; ovules 20–24(34) per locule, 2-seriate, contained within translucent, gelatinous ovule sac, 0.1–0.2 mm long, as long as or longer than funicle; funicle to 0.2 mm long, adnate to lower part of partition, style 0.5–0.6 mm long, 1.4–1.7 mm diam., similar to style type B; style apex ± flat; stigma ± lobed, 1.4 mm diam., 0.2–0.3 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins ± 4–6-sided, 0.8–0.9 mm long, 2–2.5 mm diam. at apex; thecae oblong, 0.3–0.4 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregularly 4–5-sided, sometimes clavate or prismatic, 1.6–1.8 mm long, 1.4–1.7 and 1.9–3.4 mm wide. INFRUCTESCENCE with ripe berries white.

Flowering in *Philodendron verrucosum* occurs from April through June (also September and November) in Central America. The species probably also flowers earlier in the dry season, perhaps as early as February, as suggested by the fact that a post-anthesis collection was made in March (and even in February in Colombia). Post-anthesis collections have also been made from April through July (but also in December). Immature fruits have been seen from July, October, and December. The flowering collections from September and October, as well as the immature fruits from October and December, appear to reflect bimodal flowering. On the other hand, no flowers were seen from July and no flowers or fruits from August.

Philodendron verrucosum ranges from Costa Rica to Peru at 200 to 1500 (mostly above 500) m elevation, mostly in *Premontane rain forest* and *Tropical Lower Montane rain forest* but also in *Tropical wet forest.* In Central America, it occurs principally on the Atlantic slope or near the Continental Divide in Costa Rica and Panama but also on the Pacific slope in southwestern Costa Rica. In South America, it ranges along the Pacific slope of the Andes to as far south as El Oro and Cotopaxi Provinces in Ecuador, but also occurs on the eastern slopes of the Andes in Napo and Morona-Santiago as well as in Peru in the departments of San Martín and Junín at 750 to 1850 m elevation.

Philodendron verrucosum is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is characterized by its short internodes, subterete petioles (about as long as the blades), broadly ovate-cordate blades velvety on the upper surface, and especially by the densely scaly or setose vestiture of the stems, cataphylls, petioles, and inflorescences.

Philodendron verrucosum might be confused with a few other species that have scaly parts, including

P. hammelii, P. malesevichiae, P. squamipetiolatum, and especially *P. squamicaule.* (See under the individual species for discussion of the differences.) *Philodendron squamipetiolatum* differs by its longer, more slender internodes and much smaller leaf blades (ca. 30 cm long on flowering plants) with a semi-glossy upper surface. It also differs in having solitary inflorescences (vs. usually more than one per axil in *P. verrucosum*). *Philodendron hammelii* differs in its much smaller size, petioles with foliaceous (rather than acicular) scales restricted to near the apex, and glabrous cataphylls, peduncles, and spathes. *Philodendron malesevichiae* differs by its terrestrial, creeping habit; persistent, semi-intact, glabrous cataphylls; narrowly sulcate petioles (rather than subterete as in *P. verrucosum*); and semiglossy blades lacking the conspicuous "crossveins" of *P. verrucosum.*

Additional specimens examined. COSTA RICA. **Alajuela**: Salto La Paz, 1350 m, *Ferreyra 15788* (USM); San Ramón–Balsa, ca. 2.3 km N Río Balsa, ca. 1050–1150 m, 10°11′N, 84°30′W, *Stevens 14194* (MO); ca. 4.6 km N of Río Balsa, 900–1000 m, 10°12′N, 84°31′W, *Stevens 13762* (CR, MO); 4–7 km N of Balsa, ca. 750 m, 10°13′N, 84°32′W, *Liesner & Judziewicz 14763* (MO); 2.5 km N of Balsa, 1050–1100 m, 10°11′N, 84°30′W, *Liesner & Judziewicz 14726* (CR, MO); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, ca. 850 m, *Croat 43636* (MO); 2 km N of Angeles Norte de San Ramón, 4000 ft., *Luteyn 3691* (MO); Zarcero–Quesada, 11.8 km past Zarcero, 1230 m, 10°12′N, 84°23′W, *Hoover 1352* (CR, MO); E of Río San Rafael, W of La Marina, 500 m, 10°23′N, 84°38′W, *Burger & Stolze 5041* (CR, US); Monteverde Biological Reserve, Río Peñas Blancas, 900 m, 10°18′N, 84°45′W, *Haber & Bello 8458* (CR, MO); 820 m, *Bello 2672* (CR); 850–900 m, *4478* (CR, INB); 950 m, *Bello & Méndez 2639* (CR, INB); Cantón Alfaro Ruiz, La Peña de Zarcero, *Smith 961* (F); Los Chiles–Los Angeles, San Ramón, 500–1200 m, 10°10′N, 84°30′W, *Barringer et al 2200* (CR, MO); *E. Schmidt 306* (CR). **Cartago**: 4000 ft., *J. D. Smith 391* (G); Moravia–Quebrada Platanillo, Moravia, 3–5 km from Finca Racine, 1200–1300 m, *Croat 36623* (MO); 1200–1400 m, *36795* (MO); Turrialba–Limón, along Hwy. 32, ca. 11 mi. NE of Turrialba, 850 m, *Croat 43355* (CR, MO); 31 km S of Siquirres on road to Turrialba (CR-101), 850 m, 9°57′N, 83°36′W, *Thompson & Rawlins 1163* (CM); El Muñeco, S of Río Navarro, 1400–1500 m, *Standley & Torres 51745* (CM, US); *Standley 33425* (US); Finca Navarro, 1350 m, *Maxon 636* (NY, US); 10 km S of Tapantí, 1600 m, 9°42′N, 83°46′W, *Burger & Burger 8424* (CR, F); 3.5 km SE of Tapantí, 1250 m, *Lent 851* (F, NY, US); Río Grande de Orosi, 2 km SE of Tapantí, 1350, *Lent 763* (F); 14 mi. from Turrialba, road to Pavones, *Carlson 3244* (F); Orosi, *Standley 39736* (US); La Estrella, *Standley 39547* (US); 4250 ft., *J. D. Smith 5963* (US); Río Gato, 4 km SE of Pejibaye, 700 m, 9°48′N, 83°42′W, *Liesner 14412* (MO); Tapantí Hydroelectric Reserve, 3–5 km from the gate, *D. Smith & Taylor 1009* (MO); 1300–1800 m, *Gómez 18889* (MO, RSA); Tapantí region, 1.5 km past Río Macho, along small stream along road to Humo, 1330 m, 9°17′N, 83°50′W, *Hoover 1345* (CR, MO); 4250 ft., *Cooper 5963* (CM, GH, US); Tucurrique, Las Vueltas, 635–700 m, *Tonduz 13321* (US); Reventazón Valley, Juan Viñas, *Cook & Doyle 288* (US). **Heredia**: 4 mi. N of Vara Blanca, 1350 m, *Croat 35609* (MO); 3 mi. S of Cariblanco, 760 m, *Croat 35794* (MO); La Selva Field Station, 280–300 m, 10°21′N, 84°03′W, *Schatz & Grayum 721* (DUKE). **Limón**: Cerro Chimú–Cerro Matama, 1200 m, *Gómez & Herrera 23533* (MO, US); Talamanca, Tsaki, 200 m, *Tonduz 9512* (CR, US); Fila Matama, 850 m, *Robles & Chacón 2724* (CR, MO). **Puntarenas**: Las Cruces Botanical Garden–Río Jaba, ca. 3 km SE of San Vito de Coto Brus, ca. 1050–1200 m, 8°47′N, 82°58′W, *Grayum 5621* (CR, MO); Monteverde Reserve, 1500 m, 10°17′N, 84°48′W, *Hammel & Zuchowski 13886* (MO). **San José**: San Isidro del General–Dominical, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35251* (MO); 9 mi. SW of Río Pacuar, 680 m, *Croat 35349* (MO); Bijagual, 1300 m, *Gómez 20564* (M, MO, QCA); Alto San Juan, road to Dominical, 900 m, *Molina et al. 18096* (F, NY); La Hondura, 1300–1700 m, *Standley 37783* (US); Río Claro Valley (Bajo La Hondura), below La Palma, NE of San Jerónimo, 1000–1200 m, 10°3′N, 83°58′W, *Burger et al. 9433* (CR, F, U); below La Palma NE of San Jerónimo, 1000–1200 m, 10°3′N, 83°58′W, *Burger et al. 9386* (F, MO), *Burger & Gentry 9077* (CR, F); 1500 m, 10°3′N, 83°58′W, *Burger & Stolze 5308* (CR, F), *8499* (F); Tarrazú, vic. Hormiguero, 1100–1200 m, *Croat 78935* (INB, MO). PANAMA. **Bocas del Toro**: Cerro Colorado, 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69010* (MO); Fortuna Dam area, Chiriquí Grande–Gualaca, 21.4 km past Gualaca, 8°32′N, 82°19′W, *Hoover 1327* (MO); Continental Divide, ca. 1200 m, ca. 8°45′N, 82°15′W, *McPherson 9033* (CAS, CM, K, MO); *Croat 60374* (MO); Old Bank Island, vic. of Chiriquí Lagoon, *von Wedel 1923* (MO). **Chiriquí**: Volcán Cañas Gordas, 1 m E of Cañas Gordas, *Croat 22344* (MO); Cerro Colorado, 34.1 km beyond Río San Félix, 1390 m, *Croat 37254* (MO); Gualaca–Chiriquí Grande, vic. IRHE headquarters, 1200 m, 8°45′N, 82°18′W, *Croat 66719* (MO); *66558* (AAU, MEXU, MO, NY, PMA); road to Finca Landau, 1100 m, *Correa et al. 2141* (F, MO, PMA); NW of confluence of Río Hornito and Río Chiriquí, 1050–1100 m, 8°44′N, 82°13′W, *Sytsma & Stevens 2234* (MO, PMA); Fortuna Dam, Cerro Fortuna, lower slopes, 1150 m, *Knapp & Vodicka 5576* (MO); behind Vivero Forestal, 12 km N of Los Planes de Hornito, 1200–1300 m, 8°45′N, 82°12′W, *Knapp 4949* (MO); 7 km SE of Fortuna Dam, 1100 m, *O'Connor 91-512-004* (MICH); Continental Divide, 1200–1500 m, 8°47′N, 82°13′W, *Churchill 5298* (MO); 1200 m, *O'Connor 91-511-003* (MICH); Continental Divide trail, 1200–1300 m, 8°45′N, 82°15′W, *Thompson 4954* (CM, MO). **Coclé**: El Copé region, Alto Calvario, near Continental Divide, 5 mi. N of El Copé, 900–1000 m, 8°39′N, 80°36′W, *Croat 75058* (MO); 750–900 m, *44736* (MO); 8°39′N, 80°36′W, *68768* (CM, F, MO); El Valle region, La Mesa, *Gentry 5632* (MO, PMA); 860–900 m, *Croat 37339* (MO); *13341* (MO); 900 m, *Sullivan 544* (MO); *Liesner 756* (MO); NE slopes of Cerro Caracoral, N rim of El Valle, 2700–3200 ft., *Sytsma 3787* (MO); Cerro Pilón, 5 km NE of El Valle, 800–1045 m, *Mori et al. 6633* (MO); *Lallathin 5096* (MO); Cerro Gaital, 900–1000 m, 8°40′N, 80°07′W, *Knapp 5301* (MO); 800–900 m, *Knapp & Dressler 4913* (MO); 5.6 km S of El Valle, 870 m, 8°50′N, 80°07′W, *Hoover 1319* (MO, NY); ca. 3 km N of El Valle de Antón, 850 m, *Wilbur et al. 15656* (MO). **Darién**: Cerro Pirre region, 1000–1100 m, *Hartman 4829* (MO); 9–10 km N of Alto de Nique, 1520–1560 m, *Croat 37871* (MO); Río Tuquesa, vic. of Tyler

Kittredge gold mine, ca. 2 air km from Continental Divide, *Croat 27215* (MO). **Panamá**: El Llano–Cartí, 12 mi. above Pan-American Highway, 200–500 m, *Liesner 689* (MO); Campo Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Croat 22716* (MO); Cerro Campana, 1000 m, *Nee & Stockwell 11625* (MO); *Croat 17200* (MO); ca. 850 m, 8°40′N, 79°50′W, *Thompson 4576* (MO); 850 m, *Busey 875* (MO); above Su Lin Motel, *Croat 14728* (MO); near Florida State Univ. Building, *Croat 12121* (F, MO, SCZ). **San Blas**: Cerro Habú, vic. of peak, 2500 ft., 9°23′N, 78°49′W, *Sytsma et al. 2699* (MO, US); Cerro Brewster, 850 m, 9°18′N, 79°16′W, *de Nevers et al. 5546* (MO); Cerro Obu, 400–500 m, *de Nevers et al. 8053* (MO); Nusagandi, 310 m, 9°20′N, 79°W, *Croat & Zhu 76993A* (MO). **Veraguas**: Santa Fe region, NW of Santa Fe, 11 km from Alto Piedra, Río Dos Bocas Valley, 450–550 m, *Mori et al. 3815* (MO, PMA); NW of Santa Fe, along W fork of road beyond Alto Piedra, 0.6 mi. beyond fork in the road, 1300–1350 m, *Croat 49060* (MO); Santa Fe–Río Calovébora, 0.6 mi. beyond Alto Piedra, 735 m, *Croat & Folsom 33991* (MO); 1.7 mi. past Alto Piedra, 1.5 mi. beyond Quebrada Cosilla, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76856* (MO).

Philodendron warszewiczii K. Koch & Bouché, in A. Braun et al., Append. gen. sp. Hort. berol. 1855: 4. 1855–1856. TYPE: Guatemala. San José and Florida, *Warszewicz s.n.* (holotype, B? lost?). Guatemala. Santa Rosa: Volcán Jumaytepeque, 6000 ft., *Hyde & Lux 4282* (neotype, here designated, K). Figures 16, 441–444, 446–449.

Usually terrestrial, or on rocks, sometimes epiphytic; stem appressed-climbing, thick, succulent, bare, leaf scars conspicuous, 1.5–2.6 cm long, 1.5–2 cm wide; internodes short near apex, semiglossy, glaucous, 3–5(15) cm long, 2.5–7(10)cm diam., often longer than broad lower down, dark green to gray-brown; roots pale green to dark brown, few per node, epidermis drying yellowish; cataphylls thin, soft, 18–33 cm long, weakly to sharply 2-ribbed, pale green to whitish, lightly and densely short-lineate, deciduous intact. LEAVES often deciduous in dry season; **petioles** 33–58(80) cm long, 1–2 cm diam., subterete to C-shaped, moderately soft, weakly flattened to rounded with thick, medial rib adaxially, with adaxial margins sharply raised, surface sharply striate, with a dark green ring around apex; **blades** triangular-sagittate in outline, deeply bipinnately or bipinnatisect to within 1–4 cm of the midrib, thin, semiglossy, moderately bicolorous, ± rounded at apex (the acumen 2 mm long), cordate at base, 31–78 cm long, 30–62 cm wide (0.9–1.3 times longer than wide), (1–1.3 times longer than petiole), upper surface moderately glossy, moderately paler, margins sinuate; median lobe 17–52 cm long, 23–63 cm wide, rounded to obtuse; lateral segments 1–30 cm long, 11–28 cm wide, pinnately lobed with 3 or more lobes per side, acute or acuminate; interlobal sinuses 0.78–0.94 the length of the blades; midrib flat, obscurely striate, slightly paler than surface above, raised, obscurely striate, slightly paler than surface below; basal veins 2–6 per side, with 0–1 free to base, second and third pair coalesced 2–5 cm, third and higher order veins coalesced 5–7 cm; posterior rib naked along most of its margin; primary lateral veins 3–6 per side, departing midrib at a 55–70° angle, straight to the margins, weakly raised above, raised, paler than surface below; tertiary veins raised, paler than surface above and below; minor veins visible, darker than surface below, distinctly visible on drying, arising from both the midrib and primary lateral veins. INFLORESCENCES 1(3) per axil; peduncle (2.5–3)4.5–11(16) cm long, 1–2 cm diam., dark green, dark short-lineate; **spathe** 13.5–30 cm long, 4–7.5 cm diam. (1.1–3.6(4.7) times longer than peduncle), medium to dark green throughout, blunt at apex, scarcely constricted; spathe blade short dark green lineate outside, 12 cm long, pale green to white inside; spathe tube weakly short dark green lineate outside, 14 cm long, pale green to white or purple or red inside; **spadix** sessile; white throughout, 14–24(30) cm long, constricted weakly above pistillate portion; pistillate portion 3 cm long in front, 2 cm long in back, 1.3 cm diam. at apex, 1.7 cm diam. at middle, 1.6 cm wide at base; staminate portion 8.3–15 cm long; fertile staminate portion 1.6 cm diam. at base, 1.4 cm diam. at middle, 9 mm diam. ca. 1 cm from apex; sterile staminate portion 1.3 cm diam.; pistils (1.1)4.1 mm long, 3.5–4.5 mm diam.; ovary 4–5-locular, 2.6–9.5 mm long, 3.5–4.5 mm diam., with axile placentation; locules 2.6 mm long, 0.8–1.1 mm diam.; ovule sac 2.4 mm long; ovules 3–4 per locule, 0.5 mm long, contained in thick, translucent matrix; style 1.2–1.6 mm long, 1.2–1.4 mm diam., similar to style type E; style funnel broad, moderately deep; style apex ± flat; stigma subdiscoid, unlobed, 0.7 mm diam., 0.3 mm high, lining entire upper surface of funnel; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 3.3 mm long, 1.3 mm diam. at apex; thecae oblong, 0.4 mm wide, ± parallel to one another and nearly contiguous; sterile staminate flowers rounded to somewhat clavate, irregularly 4–6-sided, 2.6 mm long, 1.3–1.8 mm wide. INFRUCTESCENCE brownish outside, brownish inside, to 3 cm wide pistillate spadix 3–7.5 cm long; berries white, 8–11 mm long; seeds 3–4 per locule, pale yellow, oblong-ellipsoid, 2–2.5 mm long, 1–1.2 mm diam., with pale raphide cells.

Flowering collections of *Philodendron warszew-*

iczii are rare, known only from May. Post-anthesis collections, concentrated between April and June (but also January, February, March, July, August, September, and December), imply that the flowering period is relatively broad, perhaps throughout the entire dry season and the first half of the rainy season. Immature fruiting collections are scattered in a somewhat bimodal pattern, one group in the mid-rainy season from July through September, the other group primarily in the early dry season from December through March (especially December and January). The immature fruits collected in November might reflect an early dry season flowering. Mature fruits are known only from this same period between December and February at the beginning of the dry season.

Philodendron warszewiczii ranges from Mexico (Jalisco and Chiapas) to El Salvador on the Pacific slope, and to Honduras and Nicaragua at 300 to 1900 m elevation, in *Tropical dry forest* life zones. In Mexico, the species occurs in "Selva Mediana Subperennifolia" and "Selva Baja Caducifolia."

Philodendron warszewiczii is a member of *P.* sect. *Polytomium.* This species is distinguished by its moderately thin, deeply dissected, bipinnatifid leaf blades and thick, succulent stems often leafless during the dry season.

Philodendron warszewiczii is most similar to *P. radiatum* and *P. dressleri.* It differs from *P. radiatum* in having thinner, more highly divided blades and thicker stems. Although both species occur in some of the same forest types in Mexico, *P. radiatum* always occupies more mesic sites within these zones. In other parts of Central America for which there are Holdridge Life Zone maps, *P. radiatum* is found mostly in *Tropical moist forest* or wetter life zones, whereas *P. warszewiczii* is known from *Tropical dry forest* areas.

Although *Philodendron warszewiczii* and *P. dressleri* occupy equally dry sites, the latter is distinguished by occurring further north in Mexico and in having the leaves divided to no more than halfway to the midrib (vs. nearly all the way to the midrib in *P. warszewiczii*).

This species occurs principally on the Pacific slope except in Nicaragua (one Honduran collection is from the Atlantic slope). This is probably due to the fact that the Continental Divide runs very near the Pacific Ocean in Nicaragua, and because there is a second, generally much higher, more centrally located range of mountains and hills that creates a rain shadow throughout most of the Pacific side of the country. Because of this, *P. warszewiczii* inhabits many sites in the central part of the country well within the Atlantic watershed.

Common names for this species include: "Guacamayo," "Cupapayo," "Mano de Lión," "Copapayo," "Ocopayo," and "Papaya de Monte" (Standley & Steyermark, 1958b).

Additional specimens examined. EL SALVADOR. S of San Salvador, *Calderón 876* (GH, US). **Ahuachapán**: Ahuachapán vicinity, 800–1000 m, *Standley 19726* (GH, NY, US). **San Salvador**: *Calderón 416* (GH, NY, US); San Salvador vicinity, 650–850 m, *Standley 19624* (NY, US). GUATEMALA. **Jalapa**: Jalapa–San Pedro Pinula, 1400–1800 m, *Standley 77055* (F). **Jutiapa**: Monjas–El Progreso, above Ovejero, ca. 1400 m, *Standley 77660* (F); near Jutiapa, ca. 900 m, *60495* (F); Agua Blanca–Amatillo, 950–990 m, *Steyermark 30367* (F); Jutiapa–La Calera, SE of Jutiapa, ca. 850 m, *Standley 76087* (F). **Santa Rosa**: near Cuilapilla, ca. 900 m, *Standley 78051* (F). **Zacapa**: upper reaches of Río Sitio Nuevo, between Santa Rosalía and first waterfall, 1200–1500 m, *Steyermark 42281* (F); Río Lima, Sierra de las Minas, Finca Alejandria, 1500–1700 m, *Steyermark s.n.* (F). HONDURAS. Río de la Orilla, SE of El Zamorano, 900 m, *Anderson & Spoehr s.n.* (MO). **Comayagua**: vic. of Comayagua, ca. 600 m, *Standley & Chacón 6021* (F). **El Paraiso**: Danlí–Los Arcos, 740–850 m, *Standley 17007* (F); near Yuscarán, 960 m, *Standley et al. 1234* (F). **Morazán**: Tegucigalpa, Guarabuqui, 2600 ft., *von Hagen & von Hagen 1272* (F, NY); S. Antonio de Occidente, 850 m, *Valerio 3654* (F); Escuela Agrícola Panamericana, 800 m, *Croat 34814* (cultivated) (MO); San Antonio de Oriente, 4 mi. N of Zamorano, *Croat 42765* (MO, US); Río de la Orilla region, SE of El Zamorano, 900–950 m, *Standley 23205* (F), *23213* (F), *23217* (F); near El Zamorano, 800 m, *Morton 7119* (US). **Olancho**: Río Olancho, San Francisco de la Paz–Gualaco, 1–4 mi. NE of San Francisco de la Paz, 690–900 m, 14°57′N, 86°13′W, *Croat & Hannon 64186* (B, MO); W of main 8.6 mi. SW of Catacamas, 400 m, 14°45′N, 86°W, *Croat & Hannon 64136* (CM, MO). MEXICO. **Chiapas**: 20–30 mi. SW of El Jocote, on road to Motozintla, 700–900 m, *Croat 40714* (MEXU, MO); Tuxtla Gutiérrez–San Fernando, Chacona canyon, 850 m, *Breedlove 69987* (CAS); 22 mi. SE of Comitán, *Carlson 1953* (F); 6–8 km E of Frontera Comalapa, road to Ciudad Cuauhtémoc, 1000 m, *Breedlove 23428* (MO); 10 km E of Mozotintla, 1110–1150 m, *Garcia et al. 1527* (MEXU, BM); vic. Tuxtla Guttierez, 830 m, *Breedlove & Bourell 68505,* (CAS); Mpio. Tzimol, 15 km S of Comitán, 1200 m, *Breedlove 51028* (CAS). **Jalisco**: Autlán–Barra de Navidad, at km 291.67, ca. 300 m, *Moore & Bunting 8744* (BH); 9 mi. N of road-junction at W end of Bahía de Navidad, 300 m, *McVaugh & Koelz 1758* (MICH); Hwy. 110, 2 mi. NE of Huizache, ca. 5 m, *Stevens & Fairhurst 1823* (US); 15–16 mi. NW of Barra de Navidad, *Dressler & Wirth 2671* (UC, US); Chamela Field Station, 100 km S of Puerto Vallarta, 50 m, 19°30′N, 105°03′W, *Gentry 63966* (MO), *Bullock 1101* (MO); El Tejón, 100 m, 19°30′N, 105°03′W, *Gentry 74426* (MO); 10 km E of Las Palmas, 340 m, 20°50′N, 105°02′W, *Cochrane et al. 12022* (MO); Reserva Biosfera Sierra de Manantlán, Lagunillas–Juluapan, Cerro Grande, ca. 1400–1500 m, 19°22′N, 103°56′30″W, *Iltis et al. 29716* (MO); Rancho Cuixmala, Cumbres 1, Arroyo Cajones, 19°27′N, 104°58′30″W, *Lott et al. 3268* (MO). **Nayarit**: Mirador de Aguila, ca. 14 mi. N of Tepic, 450–600 m, *Feddema 824* (MICH); 6–7 mi. S of Com-

postela, 1000 m, *McVaugh 18754* (MICH); 2 mi. SE of Las Varas, road to Mazatlán, 60–90 m, *McVaugh 15351* (MICH). NICARAGUA. **Boaco**: Cerro Mombachito, 8.5 km NW of Camoapa, 1059 m, *Araquistain & Moreno 931* (MO); **Chontales**: 3.9 km N of Comalapa, ca. 460 m, ca. 12°18′N, 85°30′W, *Stevens & Montiel 17206* (MO); Juigalpa–La Libertad, ca. 17.4 km NE of Río Mayales, 350–400 m, 12°12′N, 85°17′W, *Stevens 4023* (MO). **Estelí**: 10 km S of Estelí, 1000 m, *Neill 1186* (MO); km 163 on Hwy. 1, ca. 11.2 km N of entrance to Estelí, ca. 920 m, ca. 13°13′N, 86°23′W, *Stevens 11213* (MO); Cerro Cucamonga, 800–850 m, 10°15′N, 86°22′W, *Moreno 14120* (MO); Salto de Estanzuela, ca. 5 km S of Estelí, 1000 m, 13°02′N, 86°20′W, *Guzmán et al. 1189* (MO); Río La Estanzuela, 6 km al S de Estelí, ca. 1000 m, 13°01′N, 86°21′W, *Moreno 9751* (MO). **Jinotega**: Jinotega–San Rafael, ca. 2 mi. NW of Jinotega, 1000 m, *Croat 43020* (MO); Lago de Abanas, 1–2 mi. E of San Rafael de Norte–Jinotega Road, 1000 m, *Croat 42970* (MO); ca. 1 mi. SE of Yalí, 850 m, *Croat 42891* (MO). **Madriz**: San Lucas–Hacienda El Volcán, 2 km NE de San Lucas, 800–900 m, 13°25′N, 86°35′W, *Araquistain & Moreno 2018* (K, MO); Cerro Volcán de Somoto (Tepesomoto), 900–1300 m, ca. 13°25′N, 86°35′W, *Stevens & Grijalva 16389* (MO); *Araquistain & Moreno 2046* (MO); ca. 7 mi. S of Ocotal, along Highway 15, 650 m, *Croat 42797* (MO). **Matagalpa**: 5–8 mi. E of Matagalpa, 800–1000 m, *Williams et al. 24048* (F); Cerro Apante, 1000–1400 m, *Moreno 155* (MO); 1 km SE of Matagalpa, 800 m, *Vincelli 297* (MO). **Nueva Segovia**: Cerro El Achiote, 7 km N of El Jícaro, 700–1000 m, 13°46′N, 86°08′W, *Araquistain & Moreno 2316* (MO, NY); Quebrada El Nancital, ca. 6.2 km N of Ocotal, Quebrada El Nancital, 700–760 m, ca. 13°41′N, 86°24′W, *Stevens 3040* (BM, MO); 6.5 km de Ocotal, road to Las Manos, ca. 700 m, 13°40′N, 86°29′W, *Moreno 14382* (MO); El Jícaro, "Casas Viejas," ca. 600 m, 13°44′N, 86°05′W, *Moreno 13504* (MO); El Jícaro, "El Cinchado," ca. 650–700 m, 13°46′N, 86°05′W, *Moreno 13589* (MO); El Jícaro, "Río Grande," road to Murra, 460–500 m, 13°43′N, 86°W, *Moreno 13670* (MO).

Philodendron wendlandii Schott, Prod. Syst. Aroid. 221. 1860. TYPE: Costa Rica. *Wendland s.n.* (holotype, W? lost). Schott ic. 2079 (neotype, here designated). Figures 15, 450, 451, 453.

Epiphytic, sometimes occurring high in the canopy, rarely terrestrial, perhaps by accident; stem short, scurfy, leaf scars inconspicuous, 1.3–2.1 cm long, 2–2.5 cm wide, obscured by root mass; internodes short, 0.5–3 cm long, 1.8–3.5 cm diam., glaucous, epidermis fissured transversely; roots reddish green becoming dark brown, blunt, branched near tip; cataphylls somewhat spongy or fleshy, 29–36 cm long, unribbed or sometimes sharply 2-ribbed, green to reddish green, persisting semi-intact at upper nodes, eventually fibrous. LEAVES rosulate; **petioles** 9–30 cm long, 1.5–4 cm diam., broader than thick, spongy, soft, sharply flattened adaxially, sharply convex abaxially, with adaxial margins erect on younger petioles, with dark green ring at apex; **blades** oblong-oblanceolate, coriaceous, slightly bicolorous, semiglossy, acuminate, sometimes long-acuminate at apex (the acumen inrolled, 2–4 mm long), ± narrowly rounded to obtuse at base, 32–67 cm long, 8.5–22 cm wide (2.6–4.7 times longer than wide), ((1.7)2.6–4.2(5.2) times longer than petiole), broadest ± near the middle; midrib flat to convex, broadly convex near base, convex toward apex, concolorous above, round-raised to convex, slightly paler than surface below; basal veins lacking; primary lateral veins 7–12(16) per side, departing midrib at a (50)60–70° angle, ± straight to the margins, weakly impressed to sunken above, convex to weakly raised, darker than surface below; minor veins obscure above, visible, darker than surface below, arising from midrib and paralleling primary lateral veins. INFLORESCENCES erect, 2 per axil; peduncle 3–10 cm long, 1–1.5 cm diam., pale green; **spathe** erect to erect-spreading, coriaceous, 12–18 cm long ((1.5)3.4–3.6(5.3) times longer than peduncle), constricted just above the tube to 2.1 cm diam. at constriction; spathe blade oblong-ovate, pale green to white, sometimes tinged pink, sometimes white-striate outside, 7–13 cm long, 2.6–7 cm diam. when open (opening broadly elliptic in face view, white (rarely rose-red)), pale-spotted with dark green central rib inside; spathe tube ellipsoid, pale to medium green, sometimes tinged with red, white-short-lineate in back outside, (3.5)5.5–7 cm long, 2.6–3.5 cm diam., pale green to white (sometimes creamy yellow or reddish with darker green central rib), minutely pale spotted inside; **spadix** stipitate to 1.3 mm long, light green; cylindrical, bluntly pointed at apex, (8.5)11–14.4(17.2) cm long, of nearly uniform width; pistillate portion pale green to yellowish green, cylindrical, or weakly tapered toward apex, 2.9–4.6(6.7) cm long, 1–1.2 cm diam. at apex, 1.1–1.4 cm diam. at middle, 1–1.5 cm wide at base; staminate portion 8.2–11.7 cm long; fertile staminate portion creamy white, with resin droplets, 9–13 mm diam. at base, 9–12 mm diam. at middle, 6–7(9) mm diam. ca. 1 cm from apex, broadest at the base or equally broad at base and middle, as broad as the pistillate portion, as broad as to slightly narrower than the sterile portion; sterile staminate portion slightly broader than the pistillate portion, white, 1–1.3 cm diam.; pistils 1.7–2.3 mm long, 1.4–1.7 mm diam.; ovary 6–7-locular, 0.7–1.3 mm long, 1.4–1.7 mm diam., with sub-basal placentation; locules 0.7–1.3 mm long, (0.2)0.4–0.5 mm diam.; ovule sac (0.7)1–1.1 mm long; ovules 2 per locule, translucent and contained within translucent or transparent ovule sac, 0.3–0.5 mm long, longer than funicle; funicle 0.2–0.4 mm long (can be pulled free to base), style 0.6–0.8 mm

long, 1.2–1.8 mm diam., similar to style type B; style apex sloping to weakly rounded, with depressions surrounding stylar canal exits; stigma subdiscoid, truncate, 0.7–1.1 mm diam., 0.2–0.3 mm high, covering center of style apex; the androecium truncate, prismatic, margins irregularly 3–6-sided, 1.2 mm long, 0.7–1.4 mm diam. at apex; thecae ± ovate, 0.5 mm wide, ± parallel to one another, sometimes nearly contiguous, sometimes distinctly contiguous; sterile staminate flowers blunt, irregularly 4–6-sided, sometimes clavate or prismatic, 1.4–1.6 mm long, 1.1–2(3.6) mm wide. Berries bright orange.

Flowering in *Philodendron wendlandii* occurs from the mid-dry season to the first part of the rainy season, with Costa Rican populations having been found in flower earlier (February and March) than those in Panama (May and June). Post-anthesis inflorescences have been collected between February and July, with an outlying collection from November. Immature fruits have been collected only in June and August, and mature fruits in September.

Philodendron wendlandii ranges from Nicaragua to Panama, from 10 to 1250 m elevation in *Tropical wet forest* and *Premontane rain forest* life zones. Most collections are from below 800 m elevation.

Philodendron wendlandii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is distinguished by its true epiphytic habit, short stem, and rosulate, oblong-oblanceolate, short-petiolate leaves but especially by the petioles, which are often broader than thick and sharply flattened adaxially. *Philodendron wendlandii* is one of relatively few truly epiphytic, rosulate "bird's nest" species in the genus.

Philodendron wendlandii is apparently related to several species of more or less rosulate habit and with elongate leaf blades and a green or purple line of demarcation between the petiole and the blade. These include *Philodendron annulatum, P. auriculatum,* and *P. ligulatum.* With the exception of *P. ligulatum* var. *heraclioanum,* all of these taxa differ from *P. wendlandii* in having more or less terete petioles. *Philodendron ligulatum* var. *heraclioanum* itself differs in being a long-stemmed vine (vs. rosulate in *P. wendlandii*), and in having D-shaped petioles scarcely or not at all wider than thick (vs. sharply flattened and conspicuously broader than thick for *P. wendlandii*) and undulate-winged margins.

Additional specimens examined. COSTA RICA. **Alajuela**: near La Laguna, 6–8 km S of Villa Quesada, 1200 m, *Molina et al. 17553* (EAP, F, NY, US); Cañas–Upala, near Río Zapote, 1.8–2.7 km S of Río Canalete, 100 m, *Croat 36376* (MO); 8 km NE of Villa Quesada, 600 m, *Croat 46925* (MO); Río Frío, near Los Chiles, 30–40 m, 11°02′N, 84°44′W, *Holm & Iltis 826* (A, GH). **Cartago**: Moravia–Quebrada Platanillo, ca. 1250 m, *Croat 36683* (MO); 4 km S of Tucurrique, Río Vueltas, 690 m, *Lent 1096* (F). **Guanacaste**: El Silencio, near Tilarán, ca. 750 m, *Standley & Valerio 44785* (US). **Heredia**: 3 mi. S of Cariblanco, 760 m, *Croat 35833* (MO); S of Río Sarapiquí, opposite Chilamate, 60–100 m, 10°27′N, 84°04′W, *Grayum et al. 5311* (MO); La Selva Field Station, Puerto Viejo de Sarapiquí, 100–150 m, *Croat 44313* (MO); ca. 100 m, *Hammel 9086* (F, MO); *McDowell 943* (MO); *Folsom 9596* (TEX); *Hammel 8222* (DUKE). **Limón**: Finca La Suerte, *Davidson 3265* (MO); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8599* (MO, RSA); *Croat 69732* (CM, MO); Hitoy–Cerere, Quebrada Cunabrí, Baja Talamanca, 500–800 m, *Gómez 24081* (MO); Amubri, along Río Lari, 200 m, 9°29′40″N, 82°89′40″W, *Herrera 2993* (AAU, CR, MO, US); Guápiles, 850 ft., *J. D. Smith 4977* (US); Cerro Coronel, E of Laguna Danto, 20–170 m, 10°41′N, 83°38′W, *Stevens 23863* (CR, MO); E of Laguna Danto, SW towards hills E of Río Zapote, 30–170 m, 10°40–41′N, 83°38–39′W, *Stevens et al. 24988* (CR, MO); E of Río Zapote, 1 km from Río Colorado, 10–40 m, 10°40′N, 83°40′W, *Stevens & Montiel 24313* (CR, MO); *Stevens et al. 24683* (CR, MO); between Río Madre de Dios and Quebrada Cañabral, 380–440 m, 10°02′N, 83°26′W, *Grayum et al. 8712* (CR); Parque Nacional Tortuguero, NE of La Aurora, Guápiles, along Río Sierpe, 30 m, 10°22′N, 83°31′W, *Robles 2254* (CR, MO). **San José**: Carrillo Station, 700 m, *Gómez et al. 21192* (CR, MO). NICARAGUA. **Río San Juan**: Bocas de Sábalo, 70–100 m, 11°03′N, 84°27′W, *Moreno 26780* (MO). PANAMA. **Bocas del Toro**: Fortuna Dam Area, Gualaca–Chiriquí Grande, 9.4 mi. N of the Continental Divide, 175 m, 8°46′N, 82°16′W, *Croat 66819* (K, MO); 2.8 mi. N of Continental Divide, 850–950 m, ca. 8°45′N, 82°15′W, *McPherson 9653* (L, MO, PMA, US). **Colón**: Cerro Bruja from Río Escandaloso, 2000 ft., *Hammel 3205* (MO); Santa Rita Ridge, Mile 10, *Porter et al. 4740* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76962* (MO). **Panamá**: Cerro Jefe region, Campo Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Croat 22721* (MO); 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan-American Highway, 700–750 m, 9°15′N, 79°25′W, *Croat 68633* (MO); El Llano–Cartí, 10 mi. from main gate near El Llano, *Croat 33715* (CM, MO); Mile 10.1, Nusagandi, 300 m, 9°20′N, 79°W, *Croat & Zhu 76547* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río Calovébora, 0.6 mi. N of Alto Piedra, 735 m, *Croat 34141* (MO); Santa Fe–Calovébora, 1.7 mi. past Alto Piedra, 1.5 mi. beyond Quebrada Cosilla, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76820* (F, MO).

Philodendron wilburii Croat & Grayum, sp. nov. TYPE: Costa Rica. Alajuela: Cordillera de Tilarán, San Ramón–Bajo Rodríguez, vic. La Balsa, 8.9 mi. NW of center of San Ramón, 1100 m, 10°10′30″N, 84°30′W, 26 Sep. 1987, *Croat 68083* (holotype, MO–3641132; isotypes, CR, K, US). Figures 452, 454–458.

Planta plerumque hemiepiphytica; caulis scandens; internodia 3–15 cm longa, 1.3–2 cm diam.; cataphylla 7–

26 cm longa, incostata vel obtuse 1-costata, decidua; petiolus subteres vel teres, moderate spongiosus, obtuse complanatus adaxialiter, 16–55 cm longus, 5–12 mm diam.; lamina ovato-triangularis, 17–36 cm longa, 11–31 cm lata, cordata vel sagittata basi; inflorescentia 1–3(4); pedunculus 3.5–29 cm longus, 8–12 mm diam.; spatha 7.5–18 cm longa; lamina spatha extus albida vel pallide viridi aut cremeo-flava, intus albida (sub anthesi) vel cremeo-flava; tubo spathae extus virenti, intus rubella vel atrimarronino; pistilla (5)6–7-loculari; loculi 1–2-ovulati; baccae pallide vel vivide aurantiacae.

Usually hemiepiphytic, sometimes terrestrial; stem scandent, semiglossy, sap watery, spicy-scented, sometimes milky-white; internodes usually long, glossy to semiglossy, 3–15 cm long, 1.3–2 cm diam., usually longer than broad, dark green to gray-green, sometimes drying black, epidermis often cracking or minutely fissured, brittle, sometimes silver-gray; cataphylls soft, 7–26 cm long, unribbed to bluntly or sharply 1-ribbed, sometimes sharply D-shaped and sharply 2-ribbed, whitish or green, fleshy, glossy, deciduous; **petioles** 16–55 cm long, 5–12 mm diam., subterete to terete, moderately spongy or moderately firm, bluntly D-shaped or obtusely flattened adaxially, surface weakly glossy to semiglossy, smooth; sheathing 6–8 cm long; **blades** ovate-triangular, thinly coriaceous to subcoriaceous, matte to semiglossy, weakly to moderately bicolorous, acuminate to long-acuminate at apex (the acumen more or less inrolled), cordate to sagittate at base, 17–36 cm long (averaging 26 cm), 11–31 cm wide, ± equal in length to or longer than petiole, margins hyaline, upper surface drying brownish, dark brown, or gray-brown to green, lower surface drying light brownish green to reddish brown or yellowish brown; anterior lobe 11.5–32 cm long, 7–24 cm wide; posterior lobes somewhat spreading, rounded to obtuse, 4–14 cm long, (2.7)4.2–13.5 cm wide, directed toward base or somewhat outward; sinus hippocrepiform, parabolic to arcuate or arcuate with petiole decurrent, 1–6(8) cm deep; midrib broadly convex to shallowly sunken to flat, paler than surface above, convex, paler than surface, drying darker than surface below; basal veins 3–5 per side, with 0–1 free to base, 1–3(4) coalesced (0.7)1.3–4(7) cm; posterior rib naked for 0.5–2.6 cm, sometimes not naked, directed to the tip of the posterior lobe 1–3.5 cm distant from the lower margin of the posterior lobe; primary lateral veins (2)3–4 per side, departing midrib at a 40–60(70°) angle, ± straight to the margins, streaked reddish below, broadly impressed to shallowly and obtusely sunken above, weakly convex and darker than surface below; minor veins moderately distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 1–3(4) per axil; peduncle 3.5–29 cm long, 8–12 mm diam., medium green, glossy, faintly white-striate near apex; **spathe** glossy, 7.5–18 cm long, 1.4–2.2 cm diam., weakly constricted midway above the tube, 1.9–2.2 mm diam. at constriction; spathe blade creamy-white to pale green or creamy-yellow, sometimes tinged faintly reddish outside, 6–7 cm long, 2.2–3.2 cm diam. (opening 6.7–9 cm long, 3.2 cm wide), whitish (at anthesis) to creamy-yellow inside, sometimes suffused with red; resin canals orange and appearing as continuous lines at least around the throat inside; spathe tube medium to dark green and light maroon band near base, sometimes weakly to heavily tinged reddish (B & K red-purple 5/7.5), white-striate outside, 5–7.5 cm long, 2–3.6 cm diam., reddish to dark maroon (B & K red-purple 2/10) inside; **spadix** sessile; ± tapered toward apex, 6.7–11.1 cm long, broadest at or near the base, protruding strongly or weakly out of the spathe blade at anthesis; pistillate portion weakly tapered toward both ends, light green to yellowish green, (2.5)3.4–4.3 cm long in front, 2.9–3.8 cm long in back, 7–13 mm diam. at apex, 1–14 mm diam. at middle, 1–12 mm wide at base; staminate portion 5–8.4 cm long; fertile staminate portion white or light green, 10–11 mm diam. throughout, of nearly uniform diameter throughout or broadest in upper one-third, 9–13 mm diam. at base, 10–11 mm diam. at middle, 7–9 mm diam. ca. 1 cm from apex, broadest usually at the base, narrower than the pistillate portion, narrower than the sterile portion; sterile staminate portion as broad as the pistillate portion, (pre-anthesis) white to light gray, 9–14 mm diam.; pistils 1.1–2.3(3.5) mm long, 0.7–2 mm diam.; ovary (5)6–7-locular, 0.6–1.5(2) mm long, 0.8–1.3(1.6) mm diam., with sub-basal placentation; locules 0.7–1.1(2) mm long, 0.3–0.6 mm diam.; ovule sac 0.7–0.9 mm long; ovules 1–2 per locule, 2-seriate, contained within transparent, gelatinous ovule sac, 0.3–0.5 mm long, slightly longer than funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style 0.3–1.2 mm long, 0.8–1.6 mm diam., similar to style type B; style apex flat to shallowly rounded or concave; stigma brushlike to discoid or subdiscoid, purplish violet or golden honey-colored, 1–1.5 mm diam., 0.2–0.4 mm high, covering ± entire style apex; the androecium truncate, prismatic, margins irregularly 4–6-sided, 1–1.7 mm long, 0.7–1.5(2.7) mm diam. at apex; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregular, dense, 4–6-sided, prismatic, 1.5–2(2.5–3.3) mm long, (1.2)1.5–1.6(2) mm wide. Berries pale to bright orange (white, immature); seeds yellow-orange, narrowly ellipsoid.

Philodendron wilburii ranges from northern Costa Rica to the Canal Area of Panama from near sea level to 2000 m elevation. This species is highly versatile ecologically, ranging from *Premontane rain forest, Tropical Lower Montane wet forest,* and *Tropical Lower Montane rain forest* in the highlands to *Premontane wet forest* and *Tropical wet forest* life zones in the lowlands.

Philodendron wilburii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species comprises somewhat scandent plants with elongate internodes drying grayish to yellowish brown and closely fissured; mostly 1-ribbed, deciduous cataphylls; subterete petioles mostly longer than the blades; ovate to ovate-triangular blades often with the lobes directed somewhat outward; and 1–3 prominently pedunculate white to greenish inflorescences per axil.

Philodendron wilburii is probably most closely related to *P. cotonense* from the mountains of eastern Costa Rica. That species is distinguished by its yellowish-brown-drying, more narrowly triangular blades averaging over two times longer than wide and thicker stems (2.5–3 cm diam. vs. up to 2 cm diam. in *P. wilburii*). It also has typically longer peduncles (mostly more than 10 cm) and more ovules per locule (4–5, vs. 1–2 in *P. wilburii*). The two species do not overlap in their distribution, but do occur in the same life zones.

Philodendron wilburii may be confused with *P. straminicaule* from Panama, but that species differs in having thicker and shorter internodes, 1-ribbed to sharply 2-ribbed cataphylls, and larger blades (rarely less than 35 cm long, vs. rarely more than 35 cm for *P. wilburii*), with frequently more than 6 basal veins and 6 primary lateral veins (vs. no more than 5 basal veins and mostly no more than 4 pairs of primary veins for *P. wilburii*). In addition, *P. straminicaule* frequently has the peduncle shorter than the spathe and has greenish white to lavender berries (vs. having the peduncle rarely shorter than the spathe and orangish berries in *P. wilburii*). *Philodendron wilburii* is also similar to *P. smithii,* which differs in having the dried stem epidermis conspicuously yellow-brown.

This species is named in honor of Robert Wilbur (DUKE), who has made major contributions to the study of Costa Rican plants and was one of the first to collect this species.

This species is here subdivided into two varieties.

KEY TO THE VARIETIES OF *P. WILBURII*

1a. Peduncles typically equal to or shorter than the spathe, usually less than 12 cm long; leaf blades with sinus hippocrepiform to parabolic, usually drying greenish to yellowish green below; Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, Puntarenas, San José), 400–2000 m .... var. *wilburii*

1b. Peduncles typically much longer than the spathe, usually more than 12 cm long; leaf blades with sinus usually arcuate or arcuate with leaf tissue decurrent on petiole, rarely hippocrepiform, usually drying reddish brown below; Costa Rica (Cartago and Puntarenas) and Panama (Veraguas), 900–1400 m, 40–450 m along the Pacific slope ..... var. *longipedunculatum* Croat & Grayum

Philodendron wilburii Croat & Grayum var. **wilburii**

Usually hemiepiphytic, sometimes terrestrial; cataphylls 13–26 cm long, unribbed to bluntly 1-ribbed; **petioles** 16–46 cm long, obtusely flattened adaxially; blades ovate-triangular, cordate to saggitate at base, 17–36 (averaging 26) cm long, 11–27 (averaging 16) cm wide (1.3–2 times longer than wide, averaging 1.5 times), (1.3–2 times longer than petiole); sinus usually hippocrepiform, sometimes shallowly parabolic. INFLORESCENCE 1–3(4) per axil; peduncle 3.5–14 cm long; **spathe** 7.5–13.5 cm long; **spadix** 9–11 cm long; pistillate portion (2.5)3.4–4.3 cm long.

Flowering in *Philodendron wilburii* var. *wilburii* appears to have a bimodal pattern, with the main event occurring in the late dry season to the mid-rainy season (March through September but especially April through August). The second flowering event occurs in the early dry season, especially in January. A flowering collection from November is unusual. Post-anthesis collections also occur in two clusters, June through September and November through February. Mature fruits have been collected only in March.

Philodendron wilburii var. *wilburii* is largely known from central Costa Rica to an area of the frontier with Panama but rarely also to central Panama (Veraguas), extending from 400 to 2000 m, mostly at over 1000 m elevation. It is largely known from central Costa Rica, mostly at elevations of higher than 1000 m in premontane rain, lower montane wet, and lower montane rain forests. It has been collected mostly in the Cordillera de Tilarán, especially in the San Ramón region and in the Monteverde Reserve at 1350 to 1700 m (averaging at more than 1500 m) but to a lesser extent in areas to the east and west of the Central Valley. It has been collected only rarely in the Cordilleras de Guanacaste and Talamanca.

One collection believed to be this species, *Croat 76799,* is from Veraguas Province near Santa Fe in *Premontane moist forest.* Because of the isolated na-

ture of this population it may prove to represent a distinct taxon. The plants are unusual in having unribbed to bluntly 1-ribbed cataphylls; thin, ovate to ovate-triangular, cordate, mostly greenish-drying blades; and peduncles 3.5 to 14 cm long (averaging 9.3 cm long), usually equal to or shorter than the spathe.

Philodendron wilburii var. *wilburii* might be confused with a lowland form of *P. wilburii* var. *longipedunculatum* from southeastern Costa Rica that has leaf blades more nearly as broad as long (e.g., *Grayum 4759*). Especially confusing are *Grayum 4759* and *9167* from Puntarenas Province in the region of the Osa Peninsula at 300 to 400 m elevation. Both look much like *P. wilburii* var. *wilburii*, and if they prove to represent that taxon, they would be the only collections from such a low elevation and the only ones from southwestern Costa Rica.

Also noteworthy is *Croat 61199*, a sterile collection that had its locule and ovary number determined from a field-collected infructescence. This collection, from Monteverde in Puntarenas Province, Costa Rica, has ovaries with only 5 locules but 10–14 ovules per locule. It otherwise matches typical *P. wilburii*. Perhaps it represents a different species.

A collection from the Azuero Peninsula in Panama is somewhat intermediate between *P. wilburii* var. *wilburii* and *P. wilburii* var. *longipedunculatum*. Though it has very long peduncles like *P. wilburii* var. *longipedunculatum*, its blades dry somewhat blackened with the posterior lobes somewhat more rounded than normal for *P. wilburii* var. *longipedunculatum*.

Additional specimens examined for P. wilburii *var.* wilburii. COSTA RICA. **Alajuela**: San Ramón, N of Los Angeles, ca. 1200 m, *Primack et al. 236* (DUKE); between Los Angeles and ca. 4 km beyond Río Balsa, 1100–1200 m, *Utley 366* (DUKE); San Ramón–Bajo Rodriguez, 940 m, *Croat 78833* (CR, INB, MO); 1025–1100 m, *78885* (CR, INB, MO); San Ramón–Cataratas, km 11, 850 m, *Pennington 11543* (K); Cantón Alfaro Ruiz, Guadalupe, 1450 m, *A. Smith 2844* (F); San Luis de Zarcero, 1575 m, *A. Smith NY1023* (F, NY); 12 km NNW of San Ramón, 1100 m, 10°10′N, 84°29′W, *Liesner & Judziewicz 14913* (CR, MO, WIS); 15 km NNW of San Ramón by road, 2.5 km N of Balsa on road to San Lorenzo, 1050–1100 m, 10°11′N, 84°30′W, *Liesner & Judziewicz 14753* (MO); 17–20 km NNW of San Ramón, ca. 750 m, 10°13′N, 84°32′W, *14690* (MO, WIS); 1 km S of Balsa de San Ramón, 1200 m, 10°13′N, 84°31′W, *Lent 3514* (F, MO); 9 km SE of Ramón, 1000 m, 10°16′N, 84°05′W, *Loiselle 177* (MO); 11.2 km N of Zarcero, 1400 m, 10°12′N, 84°23′W, *Hoover 1351* (CR, MO); 5.7 mi. N of San Ramón, 1200 m, *Croat 46836* (MO); ca. 1.3 mi. N of Angeles Norte, ca. 1200 m, *Croat 46874* (MO); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, *Croat 43634* (CM, MO); San Ramón–Balsa, ca. 5.7 km N of bridge over Quebrada Volio, 1100–1150 m, ca. 10°08′N, 84°29′W, *Stevens 14182* (CAS, MO); 2.3 km N, Río Balsa, ca. 1050–1150 m, 10°01′N, 84°30′W, *Stevens 14198* (K, MO); Reserva Forestal de San Ramón, ca. 10 km W of Laguitos, Río San Lorencito, 850–1100 m, 10°18′N, 84°34′W, *Hammel et al. 15252* (MO); 800–1000 m, 10°12′53″N, 84°36′28″W, *Herrera & Mora 179* (MO); Río San Pedro, Cerro Azahar, 15 km NW of San Ramón by air, 1400–1500 m, 10°09′30″N, 84°34–35′W, *Liesner et al. 15486* (MO), *15487* (CR, MO, NY, WIS); UCR Reserva, Fila Volcán Muerte, 1000–1300 m, 84°32′W, 10°12′N, *Barringer & Gómez-Laurito 2559* (F), *Barringer & Pérez 3784* (CR, F); Monteverde Reserve, *Dryer 794* (MO), *997* (F); 1500–1600 m, 10°17′N, 84°47′W, *Haber et al. 10069* (CR, MO, MV); 10°18′N, 84°47′W, *Grayum & Sleeper 3851* (CR, MO). **Cartago**: Moravia-Quebrada Platanillo, ca. 1250 m, *Croat 36658* (MO); SE of Turrialba, ca. 3 km NE of La Suiza, ca. 1200 m, *Lellinger & White 1403* (US); Tapantí Reserve, *Nilsson 195* (CR), *215* (CR), *220* (CR), *238* (CR), *254* (CR), *266* (CR), *367* (CR), *647* (CR); 1250–1350 m, *Ferreyra 15702* (USM); 1500–1800 m, 9°43′N, 83°47′W, *Grayum & French 5827* (INB, MO); ca. 1350 m, 9°47′N, 83°48′W, *Grayum & Sleeper 3694* (MO, US); *Utley & Utley 5613* (DUKE); 1500–1800 m, 9°43′N, 83°47′W, *Croat & Grayum 68292* (CR, MO, US); *Croat 36122* (MO); ca. 6 km S of Cartago by air, Quebrada Cangreja, 3 km S of Pan-American Highway, 1620–1650 m, 9°46′N, 83°57′W, *Liesner & Judziewicz 14474* (MO); Alto Patillos, 4 km S of Tapantí, 1480 m, *Lent 1240* (F); Río Grande de Orosi, ca. 15 km S of Tapantí, 1500 m, 9°42′N, 83°47′W, *Burger & Liesner 6752* (F, NY); La Sierra, 6 km NE of Empalme, 2000 m, *Gómez 19762* (MO); Santa Teresa–Río Coliblanco, 6–7 km NE of Pacayas, ca. 1700 m, *Luteyn 3246* (DUKE, MO); Quebrada Honda–Río Sombrero, ca. 1–2 km above El Muñeco, ca. 1400 m, *3236* (DUKE, MO); 31 km from San José, SE on CR-2, 1750 m, *Harmon 6105* (UMO); Río Grande de Orosi valley, near Río Villegas, 1700 m, *Lent 1860* (F); Río Macho, *Nilsson 242* (CR), *274* (CR), *312* (CR). **Guanacaste**: Tilarán, Z.P. Tenorio, 1050 m, *G. Rodríguez 24* (CR). **Heredia**: Río Peje–Río Sardinalito, Volcán Barva, 700–950 m, 10°17′30″N, 84°04′30″W, *Grayum 6929* (MO); Río La Paz Grande, 7.5 km N of Vara Blanca, 1270–1350 m, *Croat 36051* (MO); La Selva Field Station, *Valerio s.n.* (USJ). **Limón**: Kámuk massif, between Río Tararia and NE Kámuk páramo, 1900–2300 m, 9°14–15′N, 82°59′W, *Davidse & Herrera 29203* (CR, MO). **Puntarenas**: Monteverde Reserve, ca. 1350 m, *Croat 47139* (MO); 2 km SW Station, 1500–1550 m, *Ingram & Ferrell-Ingram 1734* (MO); ca. 3.5 km NE of Monteverde Reserve, ca. 1500 m, *Wilbur et al. 15816* (MO); *Kennedy 545* (F); *Haber 2369* (MO); *Pounds 321* (MO); *449* (MO); *Gentry et al. 48860* (CR, MO, NY); *Haber 3880* (MO); *Haber & Bello 2458* (MO); *Bello & Cruz 5237* (CR, INB); *Croat 61199* (MO); *Feinsinger et al. 83-66-1* (FLAS); *Burger & Baker 9649* (F, MO, SEL); Palmar Norte–Jalisco, 300–400 m, 8°58′30″N, 83°28′W, *Grayum et al. 9167* (MO). **San José**: Bajo La Hondura, Paracito–Río Claro, 1100–1400 m, *Croat 44494* (F, MO); above Río Hondura, at Baja La Hondura, 1150 m, *Taylor 17933* (NY); Cerro de la Muerte, along CA-2, N of turnoff for road 222, ca. 2000 m, *Croat 32851* (MO); ca. 15 km S of San Isidro de Cartago, 1880 m, *Utley & Utley 2948* (F); La Palma, ca. 1600 m, *Standley 38300* (US); La Palma area, 1400 m, 10°12′N, 84°10′W, *Burger & Liesner 6212* (CR, F, MO); ca. 6 km NE of San Jerónimo, *Primack et al. 322* (DUKE); Braulio Carrillo National Park,

1000–1500 m, 10°05′N, 83°57′W, *Croat 61227* (CM, MO); Río Patria–Río Zurquí, Cerro Hondura, 1500–1600 m, 10°04′N, 84°01′W, *Grayum & Sleeper 6116* (CR, MO); Puriscal, Z.P. La Cangreja, 500 m, *Morales 924* (CR, INB). PANAMA. **Veraguas**: vic. Santa Fe, along road between Santa Fe and Alto Piedra, 1.7 mi. N of Hotel Santa Fe, 470 m, 8°31′N, 81°05′W, *Croat & Zhu 76799* (B, CAS, CR, F, HMNM, K, MO, NY, PMA, SCZ, US).

Philodendron wilburii Croat & Grayum var. **longipedunculatum** Croat & Grayum, var. nov. TYPE: Costa Rica. Puntarenas: vic. of San Vito de Java, ca. 1 km S of San Vito on road to Villa Neily, 8°48′N, 82°57′W, 1100 m, 13 June 1987, *Croat 66169* (holotype, MO–3610645; isotypes, CR, K, NY, US). Figures 459–464.

Planta plerumque terrestris, interdum hemiepiphytica; caulis scandens; internodia 3–15 cm longa, 1.3–1.7 cm diam.; cataphylla mollia, 7–15 cm longa, acute D-formata, plerumque acute 2-costata, decidua; petiolus subteres vel obtuse complanatus adaxialiter, 16–55 cm longa, 5–10 mm diam.; lamina 22–35 cm longa, 16–31 cm lata, triangulari-ovata, lobis posticis angustis, patentibus; inflorescentia 1–2; pedunculus 11–29.5 cm longus, 5–10 mm diam., subteres; spatha 8.7–18 cm longa, saepe viridis omnino; lamina spathae extus viridi vel flaviviridi aut eburnea vel citrina, intus pallide viridi, cremea, albida aut suffusa rubra; tubo spathae extus virenti vel atriviridi, intus atrimarronino vel atripurpureo, rubro, rubriviolaceo aut violaceo; pistilla (5)6–7(8)-locularia; loculi 1–2-ovulati; baccae aurantiacae.

Usually terrestrial, sometimes hemiepiphytic; internodes 3–15 cm long, 1.3–1.7 cm diam.; cataphylls soft, 7–15 cm long, sharply D-shaped, usually sharply 2-ribbed, sometimes unribbed or sharply 1-ribbed; **petioles** 16–55 cm long, 5–10 mm diam., obtusely flattened or bluntly D-shaped adaxially; **blades** triangular-ovate with spreading lobes, 22–35 cm long (averaging 28 cm), 16–31 cm wide (averaging 21 cm; 1.03–1.4 times longer than wide, averaging 1.3 times), (0.6–1.3 times longer than petiole); sinus usually arcuate or arcuate with decurrent petiole. INFLORESCENCES 1 or 2 per axil; peduncle 11–29.5 cm long, 5–10 mm diam.; **spathe** 8.7–18 cm long; **spadix** 6.7–11.2 cm long; pistillate portion 2.8–5.5 cm long; ovary (5)6–7(8)-locular; ovules 1–2 per locule. Berries bright orange (mature) or white (immature); seeds yellow-orange, narrowly ellipsoid.

The flowering phenology of *Philodendron wilburii* var. *longipedunculatum* is poorly known. It appears to be bimodal or, in any event, unlike the pattern of any other species. All flowering collections have been made between September and April, in the late rainy season and throughout the dry season. However, post-anthesis flowering collections from July make it obvious that some flowering also takes place during June or July, perhaps both months. Other post-anthesis collections are from January through April and also in September. The only mature infructescence was collected in March.

Philodendron wilburii var. *longipedunculatum* is known principally from eastern Costa Rica and western Panama with an outlying population at Tapantí in Cartago Province, at 900 to 1400 m elevation, especially on the Atlantic slope but also on the Pacific slope at lower elevations (40 to 450 m). The Pacific coastal populations range from Carara to the Osa and Burica Peninsulas in Puntarenas Province, with outlying populations on the Azuero Peninsula and in the Canal Area of Panama.

Philodendron wilburii var. *longipedunculatum* is distinguished by the sharply two-ribbed, deciduous cataphylls; subterete, moderately firm petioles; typically triangular-ovate blades often drying reddish to yellowish brown and usually with narrow, spreading lobes; and very long-pedunculate inflorescences.

The highland populations differ from those of the lowlands in having longer posterior lobes, which are narrower and more prominently directed outward, averaging about 11 cm long (vs. about 8 cm long for the lowland populations). The lowland populations have proportionately narrower blades (owing to their lack of long, outward-directed lobes), averaging 1.6 times longer than wide (vs. 1.3 times for highland populations).

Lowland populations in the vicinity of the Burica Peninsula have somewhat thicker blades drying with a minutely pustular or granular lower surface with the secretory ducts mostly not visible. In contrast, blades of highland populations dry darker brown to almost blackened on the upper surface and are smooth on the lower surface with the secretory ducts clearly visible and alternating with the minor veins.

The Azuero population, represented by *Croat 34476,* has leaf blades that dry somewhat blackened and have posterior lobes somewhat less narrowed and less directed outward than those of the highland Chiriquí populations. The Canal Area populations, represented by *Croat 12351* and *Croat & Zhu 77083,* also differ in having proportionately longer petioles than material elsewhere. The latter collection is also exceptional in having four inflorescences per axil.

Grayum & Sleeper 3435 is a noteworthy collection from Tapantí, Cartago Province, Costa Rica. It is unusual both in being from well out of the normal range of the variety, but also in having narrower

leaf blades and shorter peduncles. Perhaps it represents another taxon.

Additional specimens examined. COSTA RICA. **Cartago**: Tapantí Region, N of Quebrada Casa Blanca, 1300 m, 9°47′N, 83°48′W, *Grayum & Sleeper 3435* (AAU, CR, MO). **Puntarenas**: San Vito–Ciudad Neily, Fila de Cal, ca. 500–620 m, 8°41′N, 82°56′30″W, *Grayum et al. 6048* (CR, INB, K, MO, PMA); Osa Peninsula, vic. Rincón de Osa, 250–540 m, 8°42′N, 83°31′W, *Croat & Grayum 59879* (CR, MO); Quebrada Banegas–Río Riyito, ca. 7 km W of Rincón de Osa, 100–300 m, 8°41′N, 83°33′W, *Grayum 4089* (CR, MO); Rincón–Aguabuena, road to Rancho Quemado, 100 m, 8°40′N, 83°31′W, *G. Herrera 4619* (CR, INB, MO); Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1140 m, *Croat 22310* (F, MO); Río Piedras Blancas, Fila Costeña, Fila Cruces, Cerro Anguciana, 950–1150 m, 8°49′18″N, 83°11′15″W, *Grayum 10650* (CR, INB, MO); Quebrada Bonita, to ca. 1 km E of Costanera highway, Carara Reserve, 30–40 m, 9°47′N, 84°37′W, *Grayum 4759* (CR, L, MEXU, MO). **San José**: San Isidro de El General–Dominical, 4.8 mi. S of Río Pacuare, 1000 m, *Croat 35249* (CR, K, MO, PMA, US); ca. 0.5 mi. above turnoff to Canaán at Rivas, 900 m, *Croat 43429* (CR, MO); ca. 8 km SW of San Isidro de El General, 1000 m, *Williams et al. 28387* (F). PANAMA. **Bocas del Toro**: Fortuna–Chiriquí Grande, Continental Divide, 1200 m, 8°44′N, 82°17′W, *Croat & Grayum 60372* (COL, CR, DAV, IBE, K, MO, NY, PMA, S, U); 1.2 mi. N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat 60454* (MO, PMA); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60026* (B, CAS, CR, F, L, KYO, MEXU, MO, NY, PMA, R, S); Cerro Colorado, ca. 7.5 mi. from Chame Camp, 1200–1250 m, ca. 8°35′N, 81°45′W, *McPherson 8868* (MO). **Canal Area**: Pipeline Road, near R. Agua Salud, *Croat 12351* (DUKE, F, MEXU, MO, SCZ); 6 mi. N of Gamboa, Río Mendoza, 9°11′N, 79°46′W, *Croat & Zhu 77083* (CM, CR, MO, NY). **Chiriquí**: Burica Peninsula, San Bartolo Límite, 18 km W of Puerto Armuelles, 450 m, *Busey 597* (CM, CR, MO); Rabo de Puerco, 8 km W of Puerto Armuelles, 50–150 m, *Croat 21958* (F, MO); 200 m, *22482* (F, MO); Cerro Colorado, 34–35.6 km above Río San Félix, 1390–1410 m, *Croat 37250* (F, MO, NY, PMA); 28 mi. above San Félix, 1200–1500 m, *33202* (MO); Gualaca–Fortuna, 10 mi. NW of Los Planes de Hornito, 1260 m, 82°17′W, 8°45′N, *Croat 50093* (L, MO, NY); 5.9 mi. NW of Los Planes de Hornito, 1370 m, 8°43′N, 82°15′W, *Croat 49852* (MO); 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *67836* (CM, F, MO, PMA); 11.8 mi. N of Los Planes de Hornito, 1400 m, *48696* (MO); near Lago Fortuna, 1200 m, 8°46′N, 82°17′W, *Croat 74907* (MO, PMA); 1100–1200 m, 8°45′N, 82°18″W, *66565* (CM, MO); 4.8 mi. beyond IRHE Facilities at Dam, 8°46′N, 82°16″W, *Croat 68032* (MO, NY, PMA, US); trail to Río Hornito, 1100–1300 m, 8°45′N, 82°15′W, *Thompson 5003* (CM, MO); 8°45′N, 82°18′W, *Croat & Zhu 76416* (AAU, CAS, GB, MEXU, MO, SCZ, US); *76378* (MO, SCZ); N edge of lake, ca. 1100 m, ca. 8°45′N, 82°15′W, *McPherson 9081* (MO, US); 3.4 km N of Quebrada Chorro, 1.6 mi. N of center of bridge over lake, 1205 m, 8°43′N, 82°14′W, *Croat 74955* (MO); Finca Loma Linda, 1 mi. E of Cañas Gordas near Costa Rican border on road to Volcán, *Croat 23310* (F, MO). **Darién**: Parque Nacional Darién, W side of Cerro Pirre, 800–1,050 m, 7°56′N, 77°45′W, *Croat 69001* (MO). **Los Santos**: Azuero Peninsula, Jobero–Río Pedregal headwaters, 300–700 m, *Croat 34476* (MO, PMA). **Panamá**: Río Majé, ca. 4–5 mi. above waterfalls, near new Bayano Lake, <100 m, *Croat 34726* (MO).

Philodendron zhuanum Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario, vic. El Copé, ca. 6 km N of El Copé, 770 m, 8°38′N, 80°35′W, 12 July 1994, *Croat & Zhu 76755* (holotype, MO–4619357–9; isotypes, AAU, B, CAS, COL, CR, F, GH, K, MEXU, NY, PMA, QCNE, SCZ, US, VEN). Figures 465–468.

Planta hemiepiphytica; internodia 2–4 cm longa, 3–5.5 cm diam.; cataphylla 37–50 cm longa, acute 2-costata, decidua; petiolus 40–63 cm longus, obtuse D-formatus, in sicco manifeste complanatus usque 3–6 cm latus; lamina anguste ovato-sagittata, 38–62 cm longa, 27–32 cm lata; inflorescentia 3; pedunculus 9–14 cm longus, 1–1.5 cm diam.; spatha 13–18.5 cm longa, lamina spathae alba, intus suffusa magentea in triente inferiore; tubo spathae extus viridi, intus atriviolaceipurpureo; pistilla 8–9-locularia; loculi 1–3-ovulati.

Hemiepiphytic, loosely or appressed-climbing; leaf scars conspicuous, 3 cm long, 2 cm wide; internodes semiglossy, 2–4 cm long, 3–5.5 cm diam., dark green, drying dark brown, longitudinally wrinkled; roots drying light brown and weakly glossy, finely striate, epidermis peeling; cataphylls 37–50 cm long, sharply 2-ribbed, medium green, semiglossy, drying dark brown, deciduous; **petioles** 40–63 cm long (0.8–1.5 times longer than blades), bluntly D-shaped, faintly raised medially, moderately firm, medium green, surface dark green short-lineate, drying dark yellowish brown and glossy, prominently flattening to 3–6 cm wide and only a few mm thick, smooth to finely and closely striate; sheath 3–6 cm long, moderately closed; **blades** narrowly ovate-sagittate, moderately coriaceous, acuminate at apex, conspicuously sagittate at base, 38–62 cm long, 27–32 cm wide (1.8–2 times longer than wide), margins broadly undulate, much paler than surface, upper surface dark green, glossy, drying dark yellowish brown, lower surface weakly glossy, paler, drying reddish brown to yellowish green with conspicuous, dark intermittent secretory canals visible; anterior lobe 34–35 cm long, margins broadly convex, paler; posterior lobes 8.5–18.5 cm long, 7–13 cm wide, directed downward to slightly inward, broadly rounded; sinus narrow, spathulate to narrowly obovate, (7.5)15–19 cm deep, 1–3 cm wide; major veins drying with sharp ridges, usually darker than surface; midrib flat, paler than surface above, narrowly rounded, concolorous below; basal veins (3)5–6 per side, with the first free to base, numbers 3–5 coalesced (2)5–7 cm; posterior rib not at all naked or naked to 2.5 cm; primary lateral veins 6–7 per side, arising at an acute angle

then spreading to a 40–45° angle, weakly arcuate until near the margin, then turned up abruptly, weakly sunken above, convex, paler than surface below; minor veins clearly visible, arising from both the midrib and primary lateral veins, drying prominulous above, faint and weakly wrinkled below. INFLORESCENCES 3 per axil; peduncle 9–14 cm long, 1–1.5 cm diam., somewhat flattened, medium green, faintly short-lineate; **spathe** 13–18.5 cm long, margins paler; spathe blade white, except yellow-green medially on back side outside, tinged magenta on lower one-third inside; spathe tube medium green outside, dark violet-purple inside, **spadix** 11.5–18 cm long; pistillate portion creamy green, 3.5–8 cm long, 3–6 cm long in back, 1.5 mm diam. at apex, 1.9 mm diam. at middle, 1.8 mm wide at base; staminate portion 8–10 cm long; fertile staminate portion slightly narrower than the pistillate portion; sterile staminate portion barely distinguishable when fresh, 1.2–1.3 cm diam. at base, tapered only slightly upward when fresh (drying to 10 mm diam. at apex); pistils 1.9–2.1 mm long, 1.2–1.6 mm diam.; ovary 8–9-locular, 0.8 mm long, with basal placentation; locules 0.8–1.2 mm long; ovules 1–3 per locule, translucent, contained within gelatinous matrix (no true envelope), 0.3–0.4 mm long, equal in length to funicle, style similar to style type B; stylar canals emerging directly onto surface; style apex truncate; stigma short, covering entire style apex; the androecium truncate, margins irregularly 4–6 sided, 0.8–1.2 mm diam. at apex; sterile staminate flowers irregularly rounded, 0.8–1 mm wide.

Flowering in *Philodendron zhuanum* is documented by a single collection from July, at the beginning of the rainy season. A cultivated plant of the same collection flowered in November at the Missouri Botanical Garden.

Philodendron zhuanum is endemic to Panama in Coclé Province in an area of *Premontane rain forest* at 700 to 900 m elevation.

Philodendron zhuanum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is distinguished by its short, thick internodes; deciduous, sharply two-ribbed cataphylls; bluntly D-shaped petioles about as long as the blades or slightly shorter; narrowly ovate blades with prominent posterior lobes, a narrow sinus and prominently visible secretory canals; up to three inflorescences per axil; and spathes green outside and whitish inside on the blade, and dark purple-violet inside on the tube.

Philodendron zhuanum is apparently related to *P. sagittifolium* and *P. aromaticum*, differing from both in having petioles which on drying become moderately spongiose, markedly flattened (especially in the middle portions), dark yellow-brown to yellowish, and often glossy. It also differs in having conspicuous secretory canals visible in both living and dried conditions. While secretory canals are present in both *P. sagittifolium* and *P. aromaticum*, they are quite inconspicuous.

This species is perhaps most easily confused with *P. aromaticum*, which has similar leaf blades with a naked posterior rib. The latter species occurs at lower elevations and nearer the coast. In contrast, *P. zhuanum* rarely has the posterior rib naked. While *P. zhuanum* has the spathe tube dark purple-violet inside with the same color bleeding onto the lower one-third of the blade, the spathe tube of *P. aromaticum* is white to weakly maroon within and the color does not merge onto the lower part of the blade.

Philodendron zhuanum is named in honor of Guanghua Zhu, my student, field companion, and a monographer of the genus *Dracontium*, who helped to collect the type and many other aroids during our fieldwork in Panama.

Additional specimen examined. PANAMA. **Coclé**: Alto Calvario, vic. El Copé, ca. 5 mi. N of El Copé, 900–1000 m, *Croat 75054* (CM, MO).

Nomen Incertae Sedis

Philodendron auritum Lindl., J. Hort. Soc. London 8: 60. 1853.

This is perhaps an older name for *Philodendron anisotomum* but was based on a cultivated plant collected by Skinner, perhaps in Guatemala, and no specimen or illustration is known to exist to confirm that it is even a *Philodendron*. Lindley stated that it had foliage very similar to a *Syngonium* illustrated by Vellozo (1825) in *Flora Fluminensis* (vol. 10, t. 113).

Excluded Names

Philodendron armigerum Standl. & L. O. Williams, Ceiba 3: 107. 1952. = *Syngonium armigerum* (Standl. & L. O. Williams) Croat, Ann. Missouri Bot. Gard. 68: 585. 1981.

Philodendron brevinodum Standl. & L. O. Williams, Ceiba 1: 231. 1951. = *Monstera tuberculata* Lundell var. *brevinoda* (Standl. & L. O. Williams) Madison, Contr. Gray Herb. 207: 92. 1977.

Philodendron hastiferum Standl. & L. O. Williams, Ceiba 1: 232. 1951. = *Syngonium hastiferum*

(Standl. & L. O. Williams) Croat, Ann. Missouri Bot. Gard. 68: 595. 1981.

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Appendix 1. Geographic Distribution of Central American *Philodendron* Subg. *Philodendron*.

	Mex	EN	Guat	EN	Beliz	EN	El Salv	EN	Hond	EN	Nic	EN	CR	EN	Pan	ECU	VEN	AMAZ	GUIANAS	BRAZIL	PERU	BOLIVIA	CUBA	TRINIDA
advena	1		1																					
albisuccus															1									
alticola													1		1									
angustilobum									1		1		1		1									
anisotomum	1		1				1		1				1		1									
annulatum															1									
antonioanum															1									
aromaticum													1	1										
auriculatum													1	1										
bakeri													1		1									
basii	1	1																						
breedlovei	1	1																						
brenesii													1		1									
brevispathum											1		1		1	1	1	1		1	1	1		
brewsterense															1									
brunneicaule													1		1	1								
chiriquense															1									
chirripoense													1	1										
clewellii															1									
coloradense															1									
copense															1									
correae															1									
cotobrusense													1	1										
cotonense													1		1									
crassispathum													1		1									
cretosum													1		1									
davidsonii subsp. davidsonii													1		1									
subsp. bocatoranum															1									
dodsonii													1			1								
dolichophyllum															1									
dominicalense													1	1										
dressleri	1	1																						
dwyeri					1	1																		
edenudatum															1									
ferrugineum															1									
findens													1		1									
folsomii															1									

Appendix 1. Continued.

	Mex	EN	Guat	EN	Beliz	EN	El Salv	EN	Hond	EN	Nic	EN	CR	EN	Pan	ECU	VEN	AMAZ	GUIANAS	BRAZIL	PERU	BOLIVIA	CUBA	TRINIDA
fortunense															1									
fragrantissimum			1		1				1		1		1		1		1	1	1	1	1		1	1
gigas															1									
glanduliferum subsp. gland.	1		1																					
grandipes											1		1		1	1								
granulare															1									
grayumii													1		1									
hammelii															1									
hebetatum															1	1								
hederaceum var. hederaceum	1		1		1		1		1		1		1		1	1	1	1	1	1	1	1	1	1
var. kirkbridei													1		1	1			1					
var. oxycardium	1	1																						
heleniae															1									
immixtum															1									
jacquinii	1		1		1				1		1		1		1		1		1				1	
jefense															1									
jodavisianum	1		1		1				1		1		1		1	1	1							
knappiae															1									
lazorii															1									
lentii													1		1									
ligulatum var. ovatum															1									
ligulatum var. heraclioanum															1									
ligulatum var. ligulatum											1		1		1									
llanense															1									
madronense															1									
malesevichiae															1									
mexicanum	1		1						1				1		1									
microstictum													1	1										
morii															1									
niqueanum															1									
panamense															1									
pirrense															1									
platypetiolatum											1		1		1	1								
pseudauriculatum															1									
pterotum											1		1		1									
purpureoviride													1		1	1								

Appendix 1. Continued.

	Mex	EN	Guat	EN	Beliz	EN	El Salv	EN	Hond	EN	Nic	EN	CR	EN	Pan	ECU	VEN	AMAZ	GUIANAS	BRAZIL	PERU	BOLIVIA	CUBA	TRINIDA
purulhense	1		1																					
radiatum var radiatum	1		1		1		1		1		1		1		1									
var pseudoradiatum	1	1																						
roseospathum var roseo.															1									
var angustilaminatum															1									
rothschuhianum									1		1		1		1									
sagittifolium	1		1		1				1		1		1		1		1							
scalarinerve													1		1	1								
schottianum													1		1									
smithii	1		1		1				1		1													
sousae	1	1																						
squamicaule													1		1	1								
squamipetiolatum															1	1								
straminicaule													1		1									
strictum													1		1		1							
subincisum	1	1																						
sulcicaule													1		1									
tenue											1		1		1	1	1	1						
thalassicum													1		1									
tripartitum	1		1		1		1		1		1		1		1	1								
tysonii															1									
ubigantupense															1									
utleyanum															1									
verapazense	1		1																					
verrucosum													1		1	1		1				1		
warszewiczii	1		1				1		1		1													
wendlandii											1		1		1									
wilburii var wilburii													1		1									
var longipedunculatum													1		1									
zhuanum															1									
TAXON COUNT	21		15		9		5		13		18		48		82	16	8	5	4	3	4	2	3	2
ENDEMICS		7		0		1		0		0		0		6										
PERCENT ENDEMICS	33%		0%		11%		0%		0%		0%		13%		46%									
TOTAL SPECIES & SUBSPECIES	103																							
TOTAL SPECIES	95																							

Appendix 2. Technical Data on Pistils.

			H	S													
			A	T T													
			B	Y Y	#		LOCULE								OVULE		
		LEAF	I	L P	LOCULES		LENGTH		PLACEN-	OVULES/	Ovules/Locule		OVULE LENGTH		LENGTH		ENVELOPE
PHILODENDRON	Sect	BLADE	T	E E	Min	Max	Min	Max	TATION	LOCULE	Min	Max	min	max	(mm)	ARRANG	CONDITION
advena	CMM	cordate	c	B	6	7	1.30	7.00	sub	1–4	1	4	0.20	1.50	0.2-0.5 (1.5)	digittate	transl
albisuccus	PPA	cordate	c	B	5	6	5.40	5.40	axile	18–20	18	20			seeds	2-series	none
alticola	PPF	cordate	c	B	5	6	1.70	3.00	axile	12–18	12	18	0.40	0.50	0.4-0.5	2-series	none
angustilobum	TRI	3-lobed	c	B	7	8	0.90	1.20	sub	1 (2)	1	2	0.60	0.60	0.6		transp
anisotomum	TRI	3-lobed	v	B	7	8	2.70	3.20	sub	3 (4-5)	3	5	0.40	0.40	0.4	1-series	transl-gel
annulatum	CMM	oblong	c	B	7	8	0.90	2.50	sub	1-2(4-5)	1	5	0.30	1.70	0.3-1.7	1-series	transp
antonioanum	PPF	cordate	c	B	5	5	2.00	2.00	axile	25-30	25	30	0.4	0.4	0.4	2-3 series	none
aromaticum	CMM	cordate	c	B	9	10	1.80	1.80	sub	2–3	2	3	0.30	0.30	0.3	1-2 series	transl to transp
auriculatum	CGG	oblong	c	B	5	7	0.70	1.20	sub	(3)4	3	4	0.20	0.40	0.2-0.4	1-2 series	transp
bakeri	CGG	oblong	v	B	5	8	0.40	1.00	sub	1(2)	1	2	0.20	0.50	0.2-0.5		transp-gel
basii	CMP	cordate	c	D	4	6	2.00	2.00	sub	4–6	4	6	0.30	0.30	0.3	2-3 series	transp
breedlovei	PPF	cordate	c	B	5	6	0.30	0.30	axile	ca 20	20	20	0.30	0.4	0.3-0.4	2-3 series	none
brenesii	CME	cordate	c	B	6	7	1.80	1.80	sub	6–12	6	12	0.40	0.40	0.4	2-series	none-gel, matrix
brevispathum	PS	cordate	v	B	6	6	0.60	0.60	axile	6–14	6	14	0.30	0.4	0.3-0.4	2-3 series	none
brewsterense	CGG	ovate	v	D	5	5	0.60	0.60	sub	2	2	2	0.5	0.5	0.5		transp
brunneicaule	PPL	cordate	c	B	5	7	0.90	2.10	axile	(13)15-18	13	18	0.90	2.10	0.9-2.1	2-series	none
chiriquense	PPF	cordate	c	B	5	5	3.10	3.10	axile	ca. 14	14	14	0.60	0.60	0.6	2-series	none-gel, matrix
chirripoense	PC	ovate	v	B	4	6	1.40	1.40	axile	8–12	8	12	0.10	0.20	0.1-0.2	1-series	none
clewellii	CO	cordate	v	B	6	7	1.30	1.30	sub	2	2	2	0.20	0.20	0.2		transp
coloradense	CMM	cordate	c	B	4	5	1.80	1.80	axile	4–7	4	7	0.20	0.20	0.2	2-series	none-gel, matrix
copense	PPL	cordate	c	B	3	4			axile	20-22	20	22			seeds only	2-3 series	gel
correae	CGG	oblong	c/v	C	5	6	2.60	2.60	sub	1	1	1			seeds only		none
cotobrusense	TRI	cordate	c	B	6	7	1.10	1.10	sub	3	3	3	0.20	0.30	0.2-0.3	digittate	transp
cotonense	CGO	cordate	c	B	5	6	0.60	0.60	sub	4-5	4	5	0.10	0.10	<0.1	digittate	none
crassispathum	CME	subcord	c	D	6	7	5.00	8.00	axile	7-10	7	10	1.60	1.60	1.6	2-series	none
cretosum	PC	oblong	c	D	4	4	3.80	4.50	axile	20	20	20	0.20	0.60	0.2-0.6	2-3-series	none
davidsonii subsp. davidsonii	CME	subcord	c	D	8	12	1.20	2.50	sub	4-8 (10)	4	10	0.20	0.60	0.2-0.6	2-series	transl
davidsonii subsp. bocatoranu	CME	subcord	c	B	9	10	2.90	2.90	sub	6–12	6	12	0.40	0.40	0.4	2-series	transp
dodsonii	PPF	cordate	c	B	5	5	2.20	2.20	axile	20	20	20	0.30	0.40	0.3-0.4	2-series	none
dolichophyllum	CGG	oblong	c	B	7	9	1.00	2.80	sub	3–4	3	4	0.10	0.10	0.1	1-2 series	transp
dominicalense	CGO	cordate	c	B	5	6	0.70	0.70	sub	1	1	1	0.30	0.40	0.3-0.4		none-gel, matrix
dressleri	POL	cordate	c	B	4	5	2.50	2.50	axile	3-4	3	4	0.40	0.40	0.4	2-series	transl
dwyeri	CMM	cordate	c	D	7	8	0.70	0.70	basal	1	1	1	0.10	0.10	0.1		none
edenudatum	CMM	cordate	c	B	6	7	1.40	1.40	sub	3(4)	3	4	0.50	0.50	0.5	1-2 series	none-gel, matrix
ferrugineum	CMM	cordate	c	D	8	10	1.20	1.90	sub(axile)	2–4	2	4	0.40	0.50	0.4-0.5	1-series	none
findens	PPL	cordate	c	B	5	6	1.60	6.10	axile	15-20 (22)	15	22	0.30	0.50	0.3-0.5	2-series	none
folsomii	CGG	oblong	c	B	6	7	0.60	0.60	sub	1	1	1	0.20	0.30	0.2-0.3		none-gel, matrix
fortunense	PPL	cordate	c	B	7	8	1.90	1.90	sub	9–10	9	10	0.40	0.50	0.4-0.5	2-series	none
fragrantissimum	PM	cordate	c	D	7	9	1.60	2.30	axile	32-36	32	36	0.20	0.30	0.2-0.3	2-series	none-transp.
gigas	PPV	cordate	c	B	4	5	2.80	5.20	axile	20	20	20	0.10	0.10	0.1	2-3 series	none?
glanduliferum	PA	cordate	t	B	6	6	1.30	1.30	axile	10	10	10	0.50	0.50	0.5	2-series	none

Appendix 2. Continued.

PHILODENDRON	Sect	LEAF BLADE	HABIT	STYLE	# LOCULES Min	# LOCULES Max	LOCULE LENGTH Min	LOCULE LENGTH Max	PLACENTATION	OVULES/LOCULE	Ovules/Locule Min	Ovules/Locule Max	OVULE LENGTH min	OVULE LENGTH max	OVULE LENGTH (mm)	ARRANG	ENVELOPE CONDITION
grandipes	PPF	cordate	t	B	5	6	1.00	1.50	axile	16-22	16	22	0.30	0.40	0.3-0.4	2-series	none
granulare	CGG	oblong	v	E	4	5			basal	1	1	1			seeds only		
grayumii	CMM	cordate	c	B	7	8	1.00	1.30	sub	(2)3-8	2	8	0.30	0.50	0.3-0.5	2-series	transp. gel. (none)
hammelii	PA	cordate	t	B	6	6	1.00	1.00	axile	14	14	14	0.10	0.20	0.1-0.2	2-series	gel
hebetatum	PPI	cordate	c	B	5	8	1.30	4.50	axile	18-24	18	24	0.20	0.20	0.2	2-series	none
hederaceum var. hederaceum	PS	cordate	v	B	4	6	8.00	8.00	axile	20-25	20	25	0.10	0.10	0.1	2-series	none
hederaceum var. kirkbridei	PS	cordate	v	B	5	5	6.00	6.00	axile	20-25	20	25	0.10	0.10	0.1	2-series	none
hederaceum var. oxycardium	PS	cordate															
heleniae	CO	subcord	c/v	B	6	9	0.90	1.20	sub	(1)3-4	1	4	0.30	0.40	0.3-0.4	1-series	transl
immixtum	CGG	oblong	v	B	4	6	0.70	1.30	sub	1 (2)	1	2	0.40	0.70	0.4-0.7		transp
jacquinii	MAC	cordate	v	B	4	4	1.30	1.30	sub	2	2	2	0.60	1.00	0.6-1	2-series	none-gel. matrix
jefense	CMR	cordate	c	D	7	8	0.32	3.20	axile	6 seeds					seeds only	2-series	?
jodavisianum	PPF	cordate	c	B	4	6	1.20	1.70	axile	18-28	18	28	0.30	0.30	0.3	2-series	none
knappiae	CMM	cordate	c	B	4	4	0.80	0.80	axile	4	4	4	0.2	0.2	0.2	2-series	none?
lazorii	PPF	cordate	c	D	5	6	1.10	1.60	axile	10-14	10	14	0.30	0.30	0.3	2-series	none
lentii	CME	subcord	c/v	B	6	7	1.20	2.00	sub	(1-2) 4-6	1	6	0.30	0.50	0.3-0.5	1-2 series	transl
ligulatum var. ligulatum	CGG	oblong	c/v	B	6	8	0.80	2.40	sub	1	1	1	0.30	0.40	0.3-0.4		transl or gel
ligulatum var. heraclioanum	CGG	oblong	c	C	5	6	1.60	1.60	sub	2	2	2	0.40	0.50	0.4-0.5		none-gel. matrix
ligulatum var. ovatum	CGG	subcord	v	B	6	7	1.00	1.00	sub	2 (seeds)			0.4	0.4	0.4		transp
llanense	PPF	cordate	c	B	6	8	1.50	6.80	axile	(6)12-14(20)	6	20	0.20	0.30	0.2-0.3	1-2 series	transp-transl
madronense	TRI	3-lobed	c	D	6	7	2.30	2.30	sub	1	1	1			seeds only		transp
malesevichiae	PA	cordate	t	B	5	6	1.30	1.60	axile	20	20	20	.1.	0.30	0.1-0.3	2-3-series	none
mexicanum	CMM	cordate	v	B	5	7	0.90	2.50	sub	1-2(3)	1	3	0.30	1.00	0.3-0.6(1.0)	digittate	transp
microstictum	CGO	subcord	v	B	6	7	0.80	0.80	sub	1	1	1	0.4	0.4	0.4		transl
morii	CGG	subcord	c	D	4	5	1.30	1.30	sub	1	1	1			seeds only		
niqueanum	CME	cordate	c						?	?					?	?	
panamense	PPF	cordate	c	B	4	6	1.00	3.00	axile	20-31	20	31	0.30	0.30	0.3	2-series	none
pirrense	PPF	cordate	c	B	5	6	1.70	1.70	axile	20	20	20	0.20	0.30	0.2-0.3	2-series	none
platypetiolatum	CMM	cordate	v	B	7	8	0.70	1.50	sub	3	3	3	0.20	0.50	(0.2)0.4-0.5	1-series	transp-transl
pseudauriculatum	CGG	oblong	c	B	6	8	1.40	2.10	sub	1-2 (4)	1	4	0.40	0.50	0.4-0.5	1-series	transp & gel
pterotum	PPL	cordate	c	B	6	6	1.50	1.90	axile	20	20	20	0.20	0.30	0.2-0.3	2-series	none?
purpureoviride	PS	cordate	v	D	4	5	6.20	6.20	axile	15-20	15	20	0.20	0.50	0.2-0.25	2-3-series	none
purulhense	PPF	cordate	c	D	6	7	5.00	5.00	axile	13-20	13	20	0.10	0.10	0.1	2-3-series	none
radiatum var. radiatum	POL	incis-lob	c	B(C)	5	7	1.90	6.50	axile	8	8	8	0.10	0.30	0.1-0.3	2-series	transl -gel
radiatum var. pseudoradiatum	POL	incis-lob	c	B	8	8	0.60	0.60	sub	3	3	3	0.30	0.30	0.3	1-series	transp
roseospathum var. roseospathum	PC	oblong	c	B	5	7	1.40	1.40	axile	14-18	14	18	0.30	0.50	0.3-0.5	2-series	none
roseospathum var. angustilaminatum	PC	oblong	c	D	4	4	1.10	1.10	axile	6–8	6	8	0.30	0.30	0.3	1-series	none
rothschuhianum	TRI	3-lobed	c	B	5	6	0.80	0.80	sub	1	1	1	0.30	0.50	0.3-0.5		transp to gel
sagittifolium	CMM	cordate	c	B	2	3	1.00	6.30	sub	2–4	2	4	0.10	0.50	0.1-0.5	1-2 series	transl-gel
scalarinerve	PPF	subcord	c	B	4	6	0.70	3.00	axile	(10) 12-14	10	14	0.30	0.40	0.3-0.4	2-series	none
schottianum	PPF	cordate	c	B	4	6	1.90	2.50	axile	10-14(16)	10	16	0.10	0.30	0.1-0.3	2-series	transl or transp

Appendix 2. *Continued.*

			H	S													
			A	T T													
			B	Y Y	#		LOCULE								OVULE		
		LEAF	I	L P	LOCULES		LENGTH		PLACEN-	OVULES/	Ovules/Locule		OVULE LENGTH		LENGTH		ENVELOPE
PHILODENDRON	Sect	BLADE	T	E E	Min	Max	Min	Max	TATION	LOCULE	Min	Max	min	max	(mm)	ARRANG	CONDITION
smithii	CGO	cordate	c	B	7	8	0.90	1.10	basal (sub)	1	1	1	0.30	0.40	0.3-0.4		transp
sousae	CMM	cordate	c	D	6	8	0.40	1.40	basal (sub)	2	2	2	0.10	0.20	0.1-0.2		transl, transp.,gel.
squamicaule	PA	cordate	c	D	4	4	1.00	1.20	axile	20-28	20	28	0.20	0.20	0.2	1-2 series	none
squamipetiolum	PA	subcord	v	B	4	5	1.00	1.20	axile	20-30	20	30	0.10	0.20	0.1-0.2	2-3-series	none
straminicaule	CGO	cordate	c	C	5	6	0.50	2.10	sub	1	1	1	0.20	0.30	0.2-0.3		sticky, transp
strictum	PPI	cordate	c	B	5	6	1.80	1.80	axile	20-28	20	28	0.20	0.40	0.2-0.4	2-series	none
subincisum	CMM	incis-lob	c	B	4	4	0.40	0.40	axile	16	16	16	0.40	0.40	0.4	2-series	transl
sulcicaule	CGO	cordate	c	B	4	5	0.40	0.40	sub	1	1	1	0.20	0.30	0.2-0.3		transl or transp
tenue	PPF	cordate	c	B	4	5	1.60	5.90	axile	12–14	12	14	0.40	0.40	0.4	2-series	none
thalassicum	PPI	cordate	c	B	5	7	2.00	4.90	axile	16-22	16	22	0.40	0.40	0.2-0.4	2-series	none
tripartitum	TRI	3-lobed	c/v	(B)(t	6	8	0.90	2.30	sub	1-2	1	2	0.40	0.60	0.4-0.6	1-series	none-gel. matrix
tysonii	CMR	cordate	c	B	6	8	0.80	1.30	sub	(4) 5-7	4	7	0.10	0.40	(0.1) 0.3-0.4	2-series	transp
ubigantupense	CGG	oblong	v	D	8	8	1.10	1.10	sub	1	1	1	0.3	0.3	0.3		transp
utleyanum	CGG	oblong	c	?	4	5			sub	1	1	1					?
verapazense	CMM	cordate	v	D	4	6	0.90	0.90	sub	2	2	2	0.4	0.4	0.4		transp & gel
verrucosum	PA	cordate	c	B	4	5	1.90	2.50	axile	20-24(32)	20	32	0.10	0.20	0.1-0.2	2-series	transp & gel
warszewiczii	POL	incis-lob	c	C	4	5	2.60	9.50	axile	3–4	3	4	0.50	0.50	0.5	1-2 series	thick transl matrix
wendlandii	CGG	oblong	c	B	6	7	0.70	1.30	sub	2	2	2	0.30	0.50	0.3-0.5		transp or transl
wilburii var. wilburii	CGO	cordate	c/v	B	6	7	0.70	2.00	sub	1–2	1	2	0.30	0.50	0.3-0.5	1-series	transp-gel
wilburii var. longipedunculatum	CGO	cordate	c/v	B	6	7	0.40	1.50	sub	1–2	1	2	0.20	0.60	0.2-0.3(0.6)	1-series	transp-gel
zhuanum	CMM	cordate	c	B	1	3	0.80	1.20	basal	1–3	1	3	0.30	0.40	0.3-0.4	1-series	gel matrix
			c = climber														
			v = vine														
			t = terrestrial							sum	324	439	11	16			
										count	46	46	44	44			
										average	7.04	9.54	0.24	0.37			

Code	Section	Subsection	Series
PPI =	Philodendron	Philodendron	Impolita
PPV =	Philodendron	Philodendron	Velvetina
PPF =	Philodendron	Philodendron	Fibrosa
PPA =	Philodendron	Philodendron	Albisuccosa
PM =	Philodendron	Macrolonchium	
PC =	Philodendron	Canniphyllum	
PPL =	Philodendron	Platypodium	
PS =	Philodendron	Solenosterigma	
PA =	Philodendron	Achyropodium	
CMM =	Calostigma	Macrobelium	Macrobelium

Code	Section	Subsection	Series
CME =	Calostigma	Macrobelium	Ecordata
CMR =	Calostigma	Macrobelium	Reticulata
CMP =	Calostigma	Macrobelium	Pachycaulia
CGG =	Calostigma	Glossophyllum	Glossophyllum
CGO =	Calostigma	Glossophyllum	Ovata
CO =	Calostigma	Oligocarpidium	
CB =	Calostigma	Bulaoana	
CE =	Calostigma	Eucardium	
TRI =	Tritomophyllum		
POL =	Polytomium		
MAC =	Macrogynium		

Appendix 3. Sectional Composition of *Philodendron* subg. *Philodendron* in Central America with number of species in Central America.

SECTION **BAURSIA**

Section 1. *Philodendron* sect. *Baursia* (Rchb. ex Schott) Engl. in Mart. Fl. bras. 3(2): 134. 1878 ..... None

SECTION **PHILOPSAMMOS**

Section 2. *Philodendron* sect. *Philopsammos* G. S. Bunting, Phytologia 60(5): 306. 1986 ..... None

SECTION **PHILODENDRON**

Section 3. *Philodendron* (Philodendrum) Schott
- Subsection 1. *Macrolonchium* (Schott) Engl., Martius, Fl. Bras. 3(2): 139. 1878 ..... 1 sp.
- Subsection 2. *Canniphyllum* (Schott) Mayo, Bot. J. Linn. Soc. 100. 168. 1989 ..... 3 sp., 1 subsp.
- Subsection 3. *Platypodium* (Schott) Engl., Martius, Fl. Bras. 3(2): 137. 1878 ..... 5 sp.
- Subsection 4. *Psoropodium* (Schott) Engl., Martius, Fl. Bras. 3(2): 138. 1878 ..... None
- Subsection 5. *Solenosterigma* (Klotzsch ex Schott) Engl., Martius, Fl. Bras. 3(2): 139. 1878 ..... 3 sp., 3 subsp.
- Subsection 6. *Philodendron.* ..... 20 sp.
  - Series 1. *Philodendron.* ..... None
  - Series 2. *Impolita* ser. nov ..... 3 sp.
  - Series 3. *Velveta* ser. nov ..... 1 sp.
  - Series 4. *Fibrosa* ser. nov ..... 15 sp.
  - Series 5. *Albisuccosa* ser. nov ..... 1 sp.
- Subsection 7. *Achyropodium* (Schott) Engl., Martius, Fl. Bras. 3(2): 139. 1878 ..... 6 sp.

SECTION **CALOSTIGMA**

Section 4. *Calostigma* (Schott) Engl., Martius, Fl. Bras ..... 48 sp., 4 subsp.

Subsection 1. *Macrobelium* (Schott) Engl., Martius, Fl. Bras. 3(2): 143. 1878.
- Series 1. *Macrobelium.* ..... 16 sp.
- Series 2. *Ecordata* ser. nov ..... 5 sp., 2 subsp.
- Series 3. *Reticulata* ser. nov ..... 2 sp.
- Series 4. *Pachycaulia* ser. nov ..... 1 sp.

Subsection 2. *Glossophyllum* (Schott) Croat, comb. nov.
- Series 1. *Glossophyllum* Schott ..... 15 spp., 3 subsp.
- Series 2. *Ovata* ser. nov ..... 7 spp., 2 subsp.

Subsection 3. *Oligocarpidium* Engl., Engler's Bot. Jahr. 26: 535. 1899 ..... 2 spp.

Subsection 4. *Bulaoanum* Mayo, Bot. J. Linn. Soc. 100: 168. 1989 ..... None

Subsection 5. *Eucardium* (Engl.) Mayo, Bot. J. Linn. Soc. 100: 168. 1989 ..... None

SECTION **TRITOMOPHYLLUM**

Section 5. *Tritomophyllum* (Schott) Engl., Martius, Fl. Bras. 3(2): 144. 1878 ..... 6 spp.

SECTION **SCHIZOPHYLLUM**

Section 6. *Schizophyllum* (Schott) Engl., Martius, Fl. Bras. 3(2): 144. 1878 ..... None

SECTION **POLYTOMIUM**

Section 7. *Polytomium* (Schott) Engl., Martius, Fl. Bras. 3(2): 145. 1878 ..... 3 spp., 2 taxa

SECTION **MACROGYNIUM**

Section 8. *Macrogynium* Engl., Bot. Jahrb. 26: 553. 1899 ..... 1 sp.

SECTION **CAMPTOGYNIUM**

Section 9. *Camptogynium* K. Krause, in Engler, Das Pflanzenreich IV. 23Db (Heft 60): 3, 127. 1913 ..... None

Appendix 4. Phenological Patterns of Central American *Philodendron* subg. *Philodendron*.

	Flowering Pattern						
PHILODENDRON	All Year	Wet	Wet->Dry	Dry	Dry-> Wet	BiModal	Unknown
advena	1						
albisuccus		1					
alticola					1		
angustilobum					1		
anisotomum			1				
annulatum					1		
antonianum		1					
aromaticum						1	
auriculatum					1		
bakeri				1			
basii		1					
breedlovei		1					
brenesii					1		
brevispathum					1		
brewsterense				1			
brunneicaule					1		
chiriquense		1					
chirripoense				1			
clewellii					1		
coloradense		1					
copense						1	
correae		1					
cotobrusense		1					
cotonense					1		
crassispathum					1		
cretosum					1		
davidsonii subsp. davidsonii					1		
subsp. bocatoranum+A50		1					
dodsonii		1					
dolichophyllum					1		
dominicalense		1					
dressleri		1					
dwyeri				1			
edenudatum				1			
ferrugineum		1					
findens					1		
folsomii				1			
fortunense					1		
fragrantissimum					1		
gigas		1					
glanduliferum subsp. glanduliferum		1					
grandipes					1		
granulare		1					
grayumii					1		
hammelii		1					
hebetatum					1		
hederaceum var. hederaceum	1						
var. kirkbridei					1		
var. oxycardium							1
heleniae					1		
immixtum					1		
jacquinii		1					

Appendix 4. Continued.

	Flowering Pattern						
PHILODENDRON	All Year	Wet	Wet->Dry	Dry	Dry-> Wet	BiModal	Unknown
jefense		1					
jodavisianum					1		
knappiae				1			
lazorii					1		
lentii					1		
ligulatum var. ligulatum							1
var. heraclioanum							1
var. ovatum							1
llanense					1		
madronense		1					
malesevichiae					1		
mexicanum					1		
microstictum					1		
morii						1	
niqueanum		1					
panamense					1		
pirrense		1					
platypetiolatum					1		
pseudauriculatum					1		
pterotum					1		
purpureoviride	1						
purulhense		1					
radiatum var radiatum	1						
var pseudoradiatum	1						
roseospathum var roseospathum					1		
var angustilaminatum		1					
rothschuhianum					1		
sagittifolium					1		
scalarinerve					1		
schottianum					1		
smithii					1		
sousae		1					
squamicaule		1					
squamipetiolatum					1		
straminicaule					1		
strictum					1		
subincisum							1
sulcicaule					1		
tenue					1		
thalassicum					1		
tripartitum					1		
tysonii					1		
ubigantupense		1					
utleyanum		1					
verapazense					1		
verrucosum					1		
warszewiczii					1		
wendlandii					1		
wilburii var wilburii						1	
var longipedunculatum			1				
zhuanum		1					
TOTAL	5	29	2	7	51	4	5

Appendix 4. Continued.

	Flowering Pattern						
PHILODENDRON	All Year	Wet	Wet->Dry	Dry	Dry-> Wet	BiModal	Unknown
% of Total	4.85%	28.16%	1.94%	6.80%	49.51%	3.88%	4.85%









Figures 1–4. —1 (top L). *Philodendron radiatum*, showing adventitious roots. Cultivated at Summit Gardens. —2 (top R). *P. schottianum* (*Croat 66395*), showing stems with transverse fissures and coarse striations at apex of node. —3 (bottom L). *P. malesevichiae*, showing trichome-like scales (*Croat 76707*). —4 (bottom R). *P. rothschuhianum*, showing stems that dry with minute cracks and scurfy condition (*Croat 57199*).

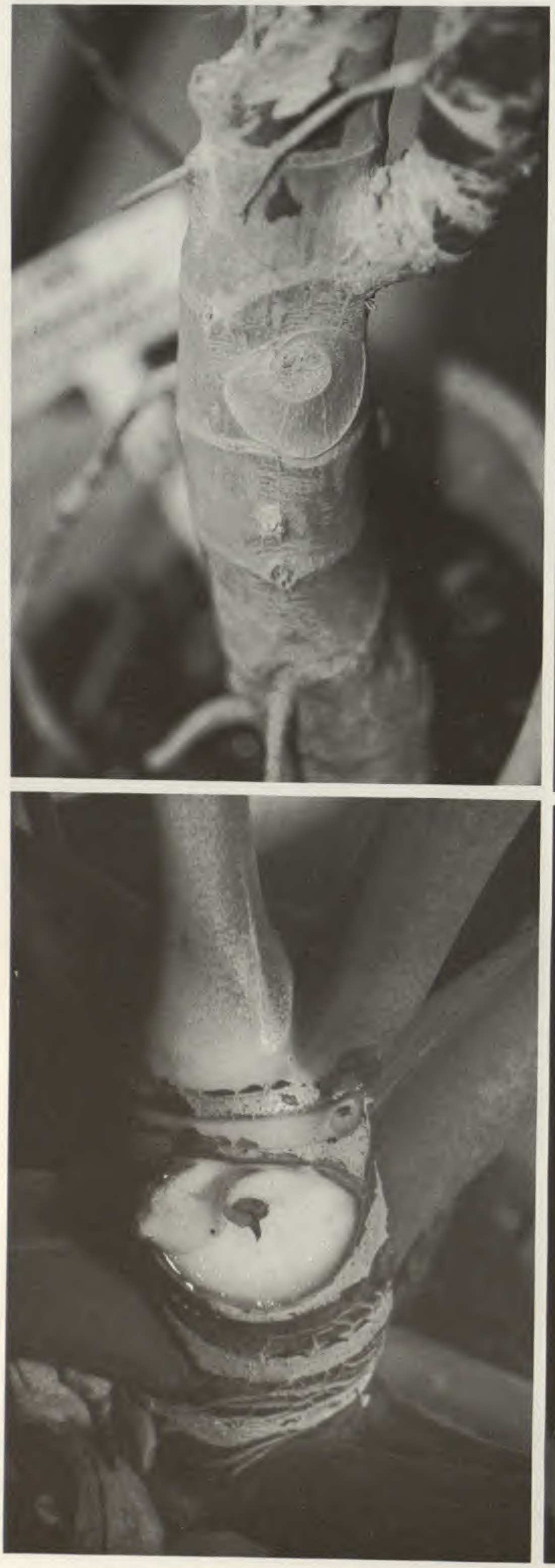


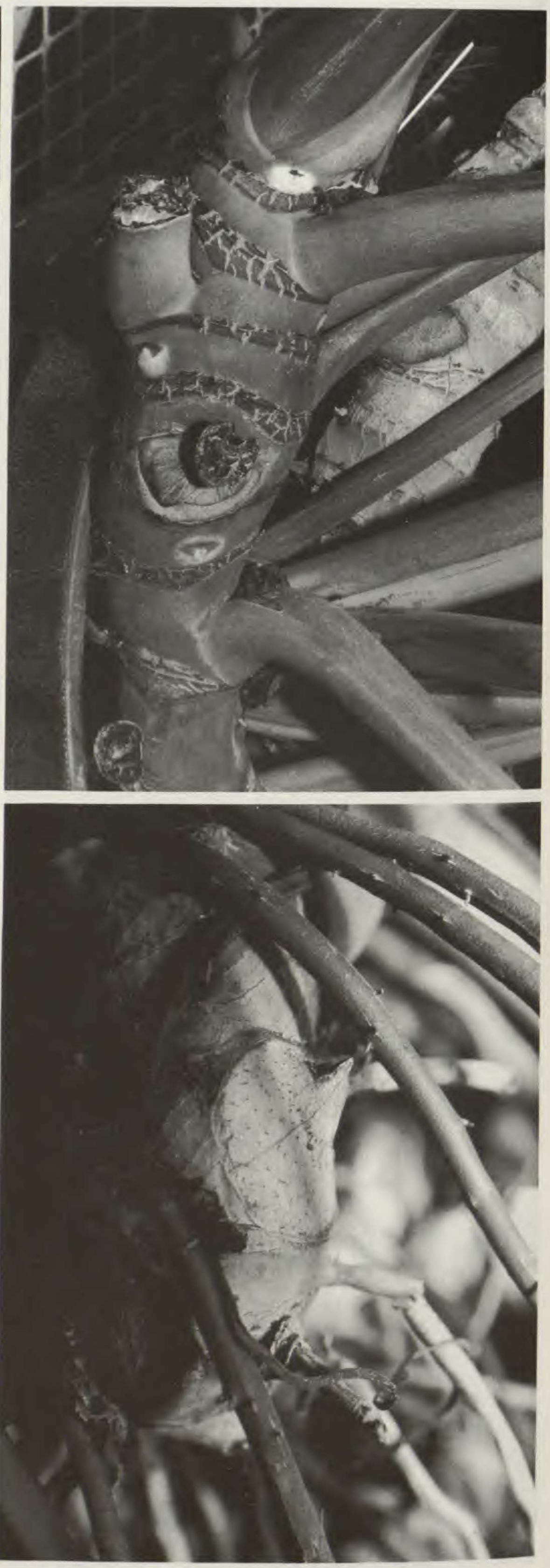






Figures 5–8. —5 (top L). *Philodendron conforme* (Venezuela), showing stems with transverse fissures at points of stress, petiole scar, and scar of inflorescence (*Croat 59355*). —6 (top R). *P. straminicaule*, dried stem showing conspicuous ribbing caused by drying (*Croat & Grayum 60057*). —7 (bottom L). *P. findens*, dried stem showing interruption of conspicuous epidermis by petiole base (*Croat 66811*). —8 (bottom R). *P. radiatum* Schott var. *pseudoradiatum*, showing stems with cracking and protruding epidermis (*Croat & Hannon 63381*).





Figures 9–12. —9 (top L). *Philodendron rothschuhianum*, showing inconspicuous cataphyll scars and petiole scars (*Croat 57199*) (photo: P. Malesevich). —10 (top R). *P. davidsonii* (*Davidson 3956*), showing stem with conspicuous cataphyll scars and petiole scars. —11 (bottom L). *P. megalophyllum* (*Croat 54252*), stem with intravaginal squamulae occurring just above the cataphyll scar. —12 (bottom R). *P. auriculatum* (*Croat 59730*), stem with spreading anchor roots showing spinelike root branch buds.











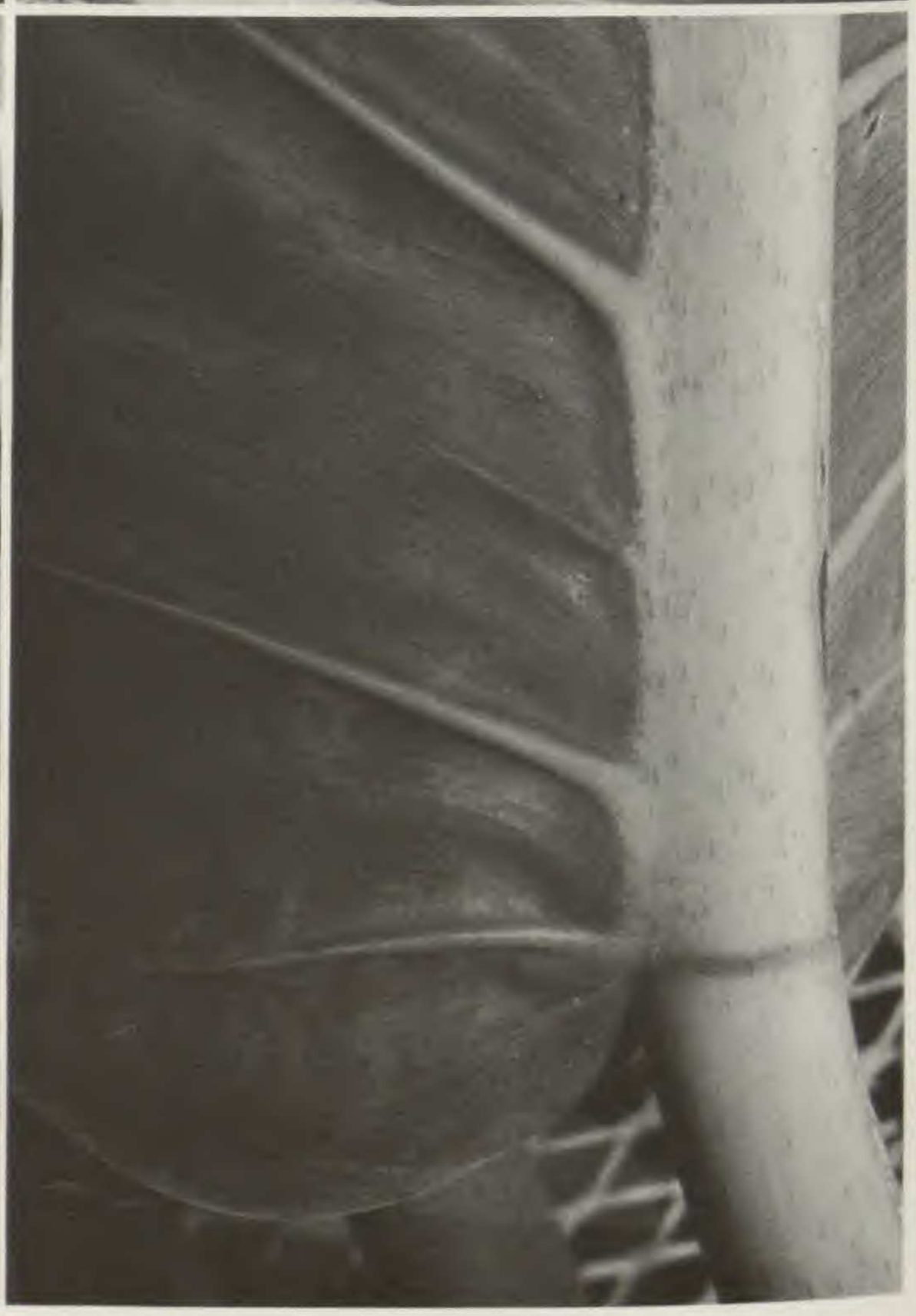


Figures 13–16. 13, 14. *Philodendron lazorii* (*Croat 69833*). —13 (top L). Showing clasping roots closely appressed to tree. —14 (top R). Showing clasping roots and a much larger feeder root. —15 (bottom L). *P. wendlandii*, showing persistent, intact cataphylls held in place by contiguous petioles (*Croat 69732*). —16 (bottom R). *P. warszewiczii*, showing weakly 2-ribbed, short-lineate cataphyll (*Croat & Hannon 64186*).









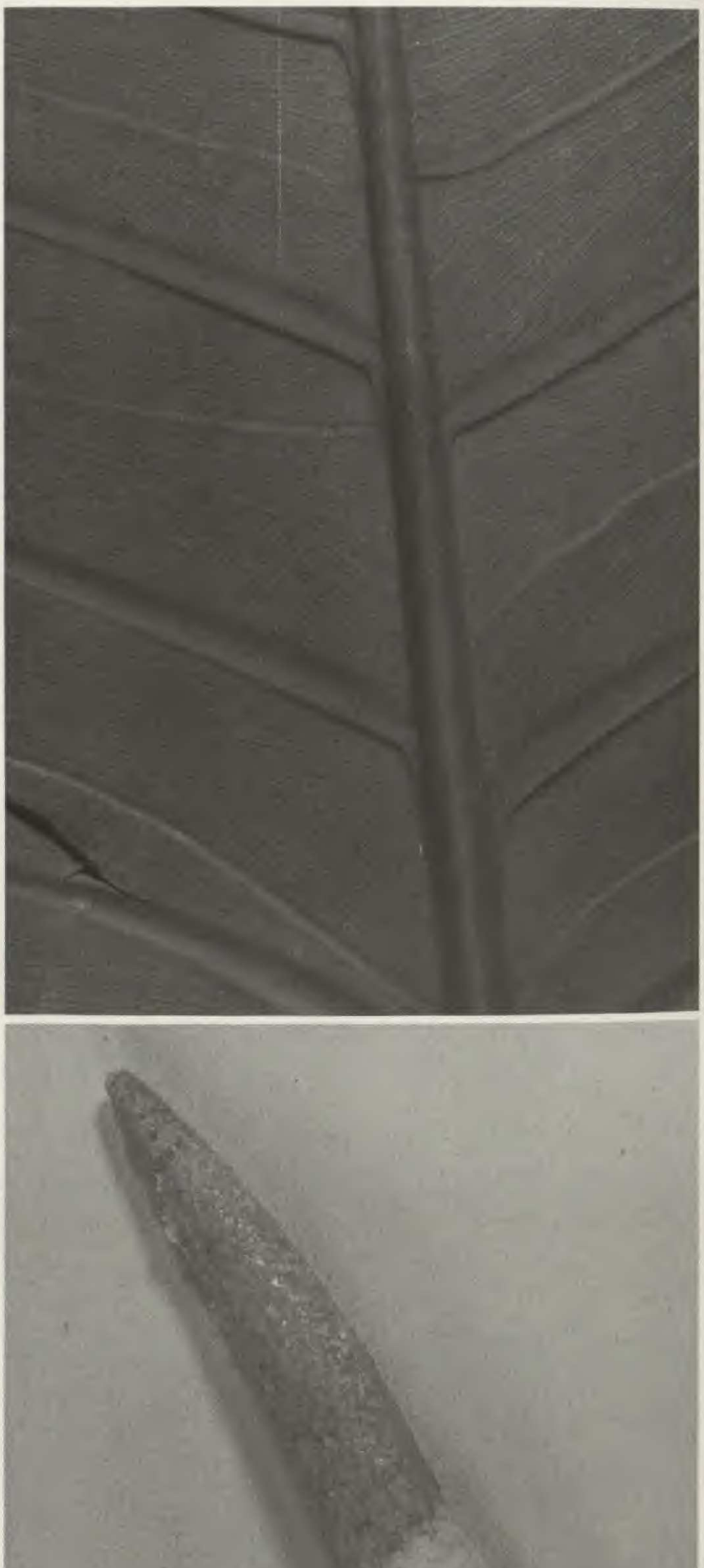
Figures 17–20. —17 (top L). *Philodendron schottianum*, showing bluntly 2-ribbed cataphyll (*Croat & Zhu 76518*). —18 (top R). *P. megalophyllum*, showing petioles which are narrowly sulcate with broadly rounded margins (*Croat 54252A*). —19 (bottom L). *P. davidsonii* subsp. *bocatoranum*, showing sweet, viscid droplets and combination of short-lineate and lineate-streaked markings (*Croat 38177*). —20 (bottom R). *P. auriculatum*, showing dark green ring demarcating petiole and blade and free basal veins (*Croat & Grayum 59730*).



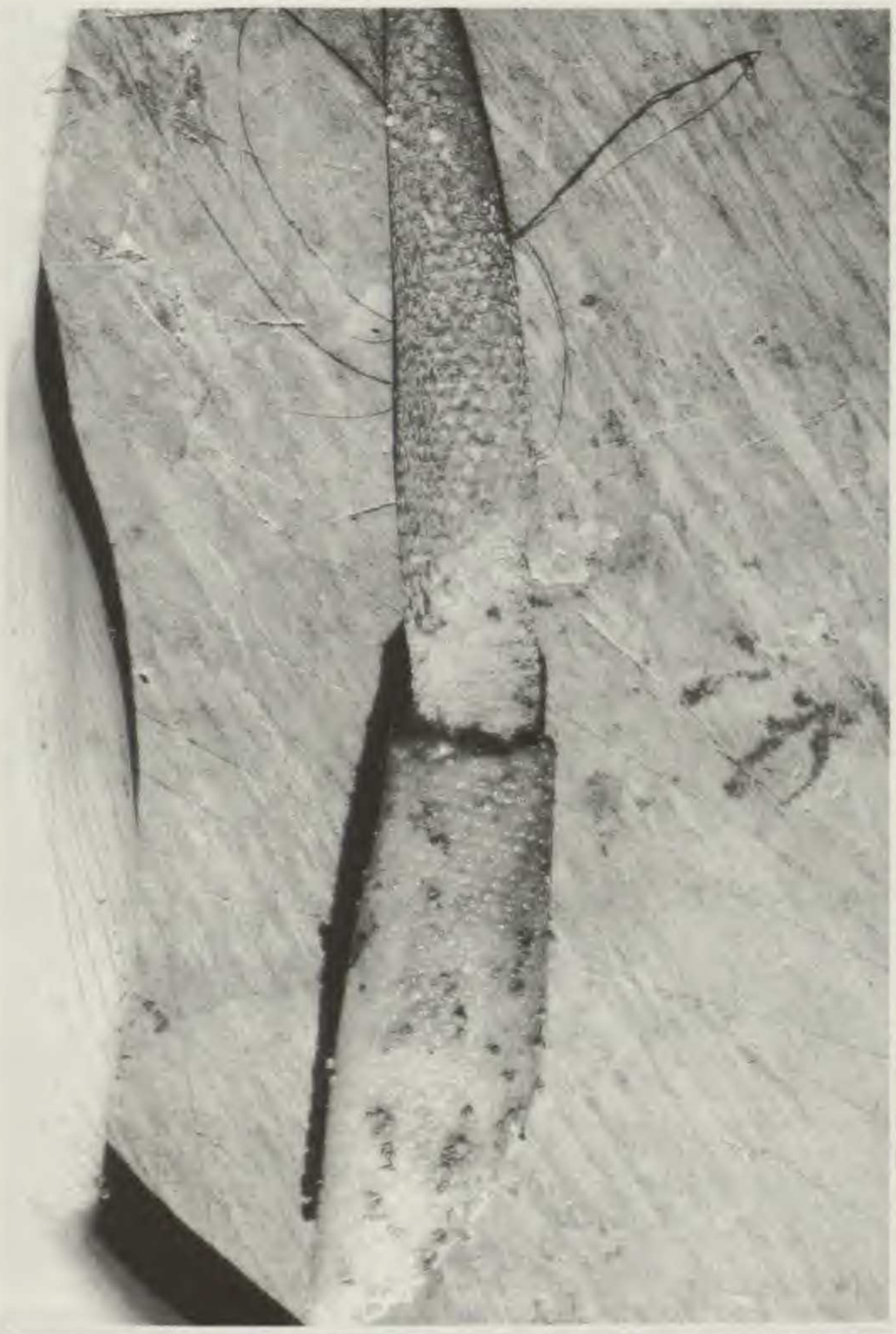


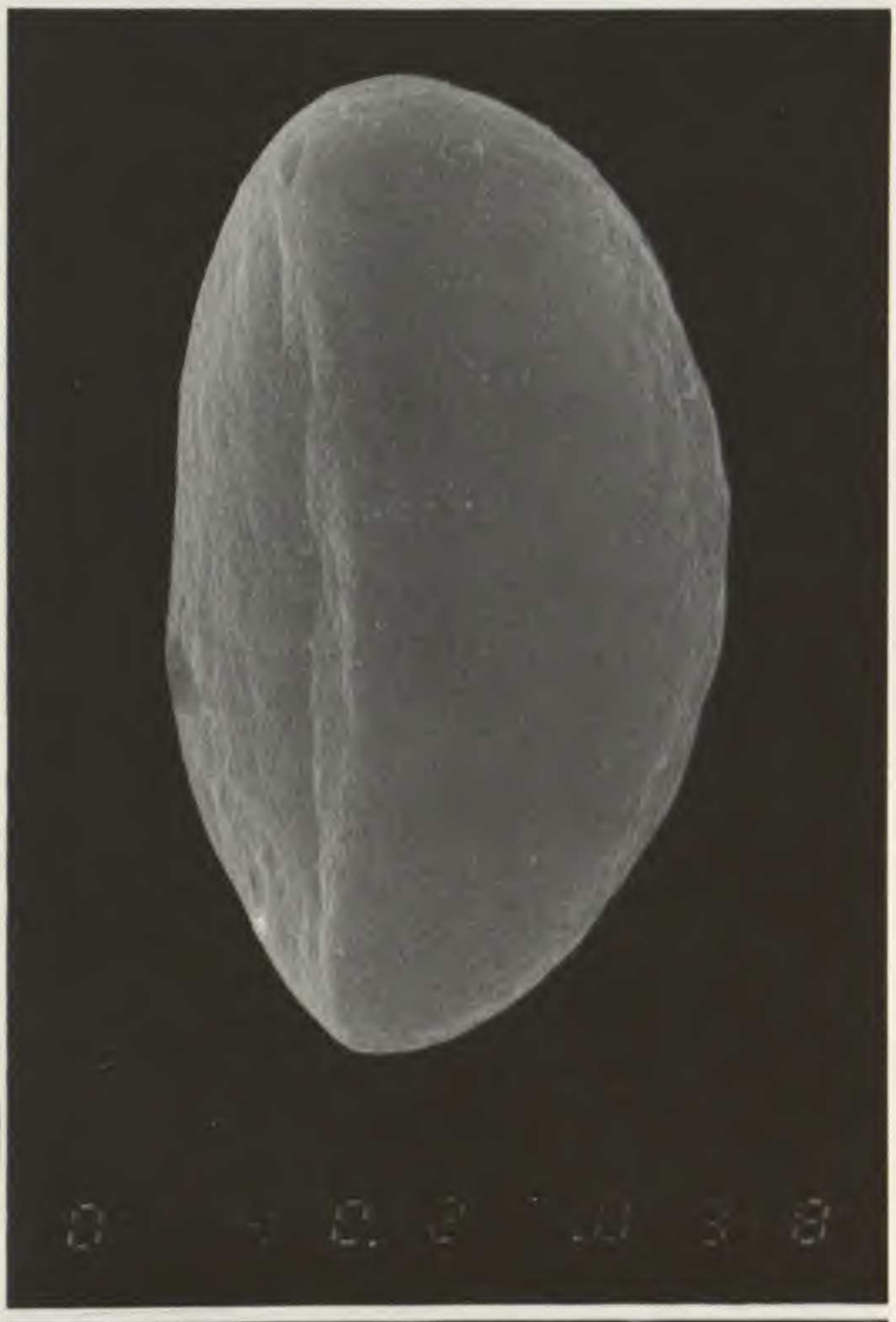
Figures 21–24. —21 (top L). *Philodendron malesevichiae*, showing snapped petiole with slender strands of latex (*Croat & Bay 75810*). —22 (top R). *P. giganteum* (*Croat 68568*), showing midrib, primary lateral veins, and basal veins (the lowermost primarily fused to form posterior rib). —23 (bottom L). *P. auriculatum*, showing quilted primary lateral veins (*Croat & Grayum 59730*). —24 (bottom R). *P. megalophyllum*, showing arrangement of veins: midrib, primary lateral veins with lowermost branching (these secondary veins), and interprimary veins (*Croat 53901*).





Figures 25–28. —25 (top L). *Philodendron malesevichiae*, showing lowermost primary lateral veins and basal veins (these loosely coalesced toward the base) (*Croat 74818*) (photo: P. Malesevich). —26 (top R). *P. megalophyllum*, showing minor veins arising from the midrib and primary lateral veins (*Croat 53901*). 27, 28. *P. malesevichiae* (*Croat & Zhu 76707*). —27 (bottom L). Fresh spadix with pistillate flowers at base, sterile staminate flowers in middle, and a portion of the fertile staminate spadix at apex. —28 (bottom R). Older spadix showing the discolored staminate spadix and white sterile staminate portion.









Figures 29–32. —29 (top L). *Philodendron tysonii*, showing spadix with sterile male flowers having been consumed by beetle pollinators (*Croat 67577*). —30 (top R). *P. fragrantissimum*, pollen grain (*Grayum 2436*, DUKE). Photo: M. H. Grayum. —31 (bottom L). *P. rothschuhianum*, showing strands of pollen emerging from anthers (*Croat 35657*). —32 (bottom R). Insect visitors to newly opening spadix of *P. anisotomum*. Large beetles shown (*Erioscelis colombica*) are legitimate pollinators; smaller insects (*Neella*, order *Hemiptera*) are frequent visitors to *Philodendron* but play no known role in their biology. Photo: H. Young.





Figures 33–36. —33 (top L). *Philodendron hebetatum*, showing spathe beginning to break up to expose mature berries (*Croat & Monsalve 61396*). —34 (top R). *P. findens*, showing scar left by fallen spathe and coarsely striate peduncle apex (*Croat 38218*). —35 (bottom L). *P. pseudauriculatum*, showing mature infructescences with spathe and staminate portion of spadix fallen (*Croat & Zhu 76251*). —36 (bottom R). *P. brenesii*, showing infructescence with exfoliating spathe and partially consumed berries (*Croat 35519*).







Figures 37–40. *Philodendron advena.* —37 (top L). (*Croat & Hannon 63107*) Adult blade. —38 (top R). (*Croat & Hannon 65549*) Stem with two pre-anthesis inflorescences and semipersistent cataphylls and an elongated petiole sheath. —39 (bottom L). (*Croat & Hannon 63107*) Infructescences (one showing spathe already fallen). —40 (bottom R). (*Croat & Hannon 63430*) Infructescence nearing maturity (showing cut open view). Because of oblique attachment, adaxial side of spadix is longer than the abaxial side.









Figures 41–44. 41–43. *Philodendron albisuccus*. 41, 42 (top L & R). (*Croat 37851*). —43 (bottom L). (*Croat 68940*). —44 (bottom R). *P. anisotomum* (*Croat & Hannon 64364*).













Figures 45–48. *P. alticola* (*Croat 74906*). —45 (top L). Stem with post-anthesis inflorescence. —46 (top R). Juvenile and pre-adult leaves. —47, 48 (bottom L & R). Adult leaves.









Figures 49–52. *Philodendron angustilobum.* —49 (top L). (*Croat 61162*) Habit, in cultivation. —50 (top R). Plants displaced from trees, with inflorescences (*Croat & Hannon 64522*). 51, 52. (*Croat 61162*). —51 (bottom L). Inflorescence at anthesis. —52 (bottom R). Habit in cultivation.









Figures 53–56. *Philodendron anisotomum*. —53 (top L). Habit in cultivation (Berlin Botanical Garden (031-60-74-83)). —54 (top R). Stem with anchor roots spreading from stem. —55 (bottom L). Leaf in cultivation (*Croat & Hannon 64364*). —56 (bottom R). Plant with inflorescence in cultivation (*Selby 80-1668*, from Mexico, Chiapas, Ocosingo).



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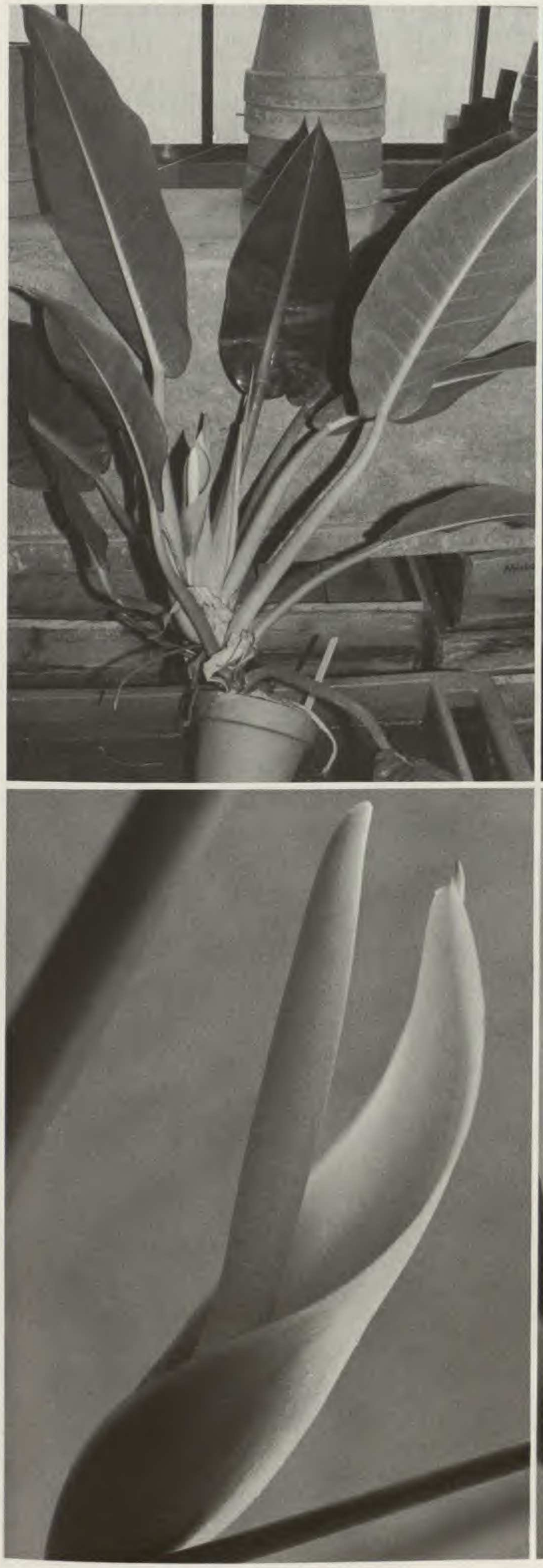


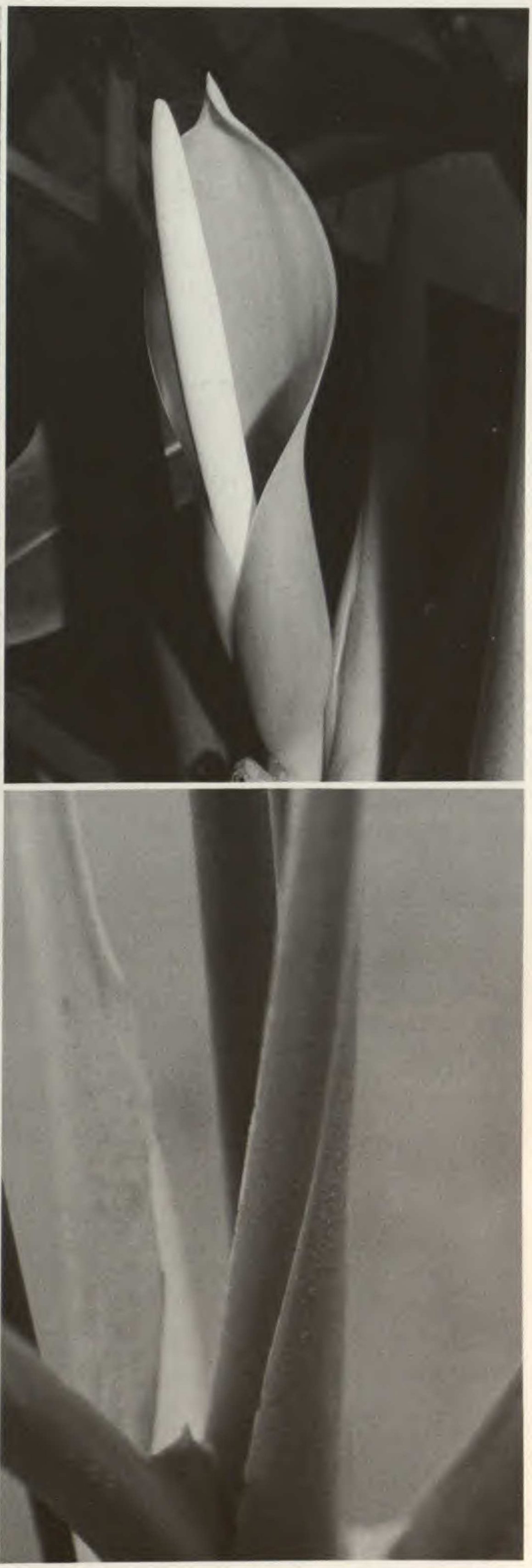




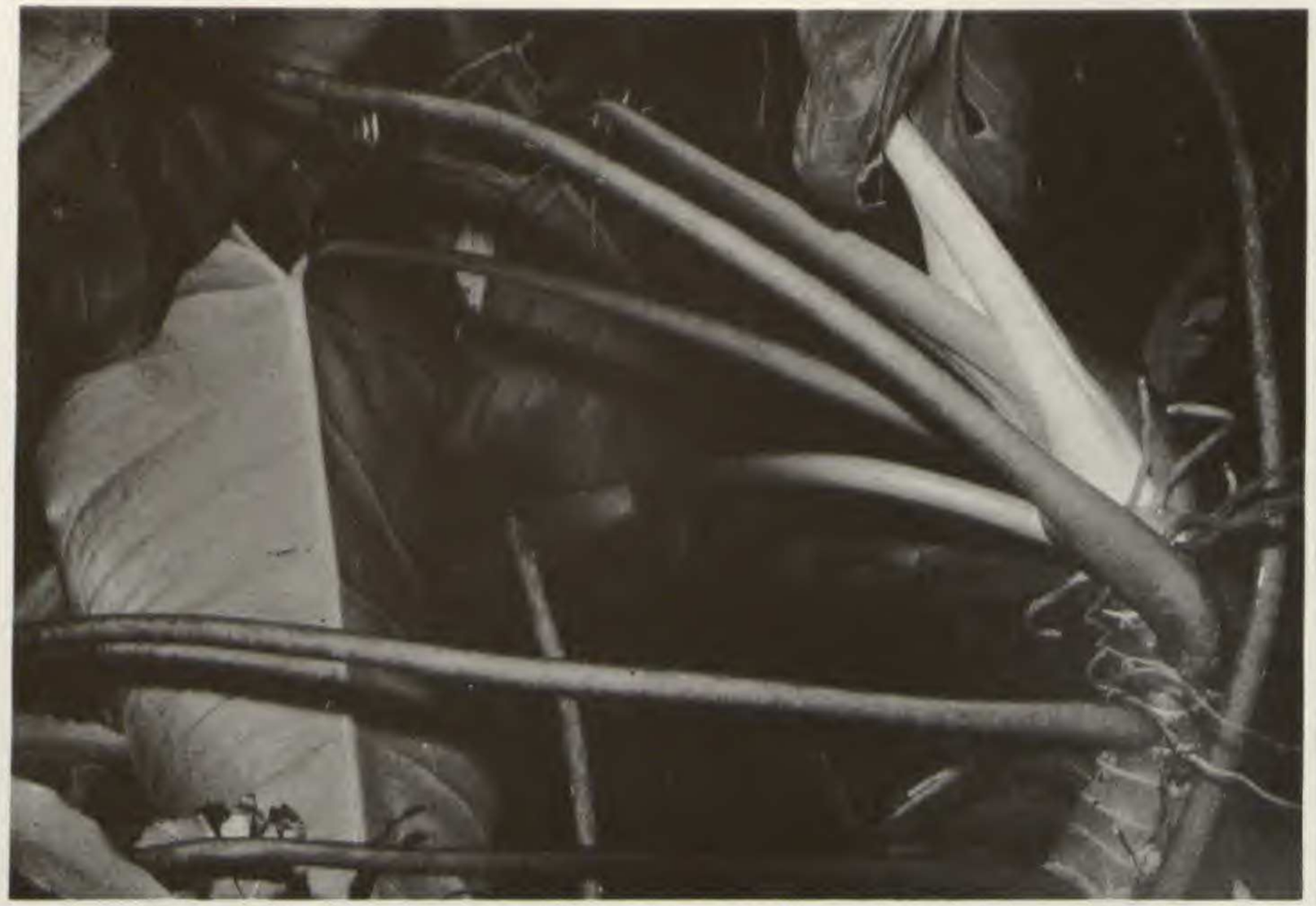


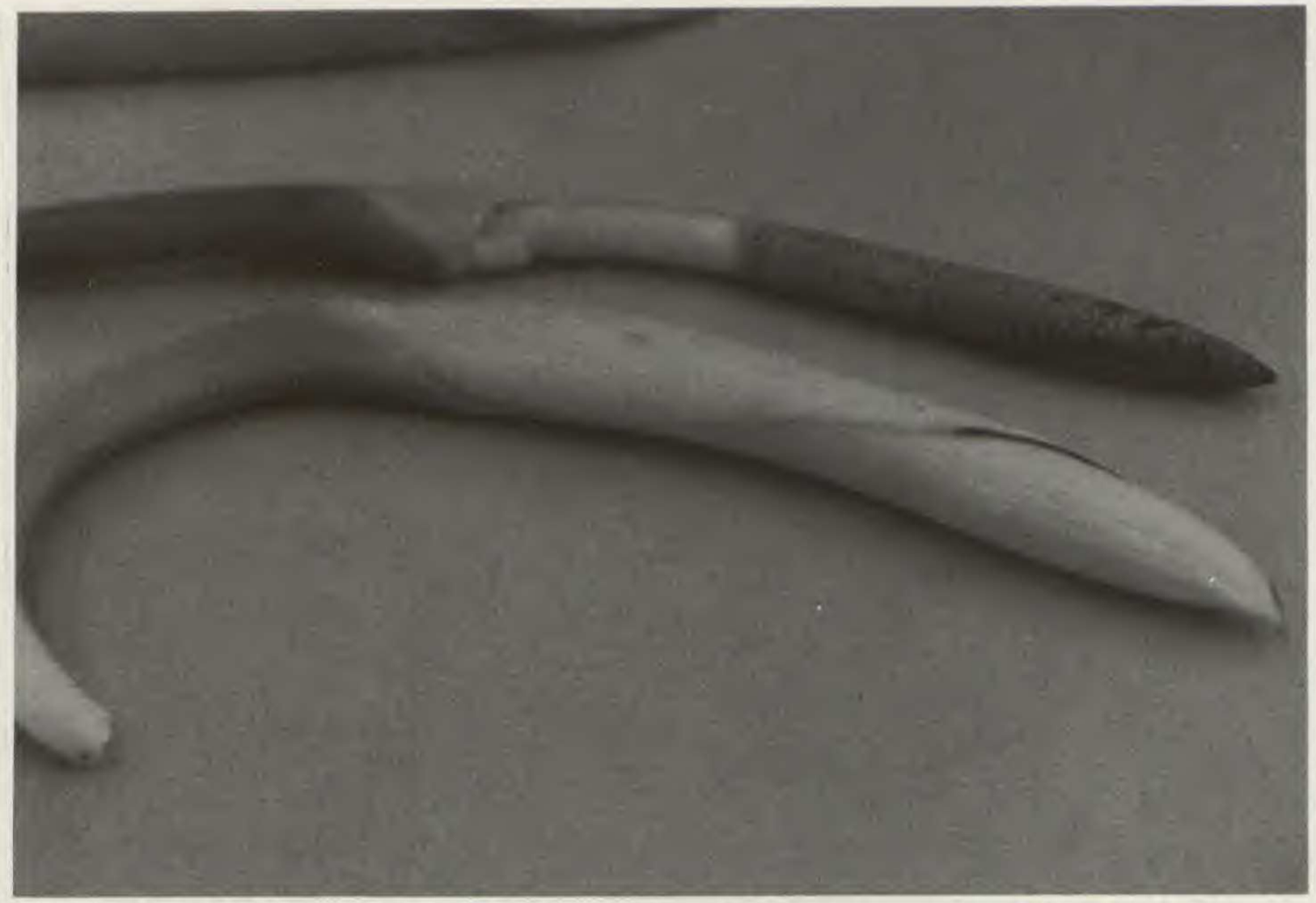
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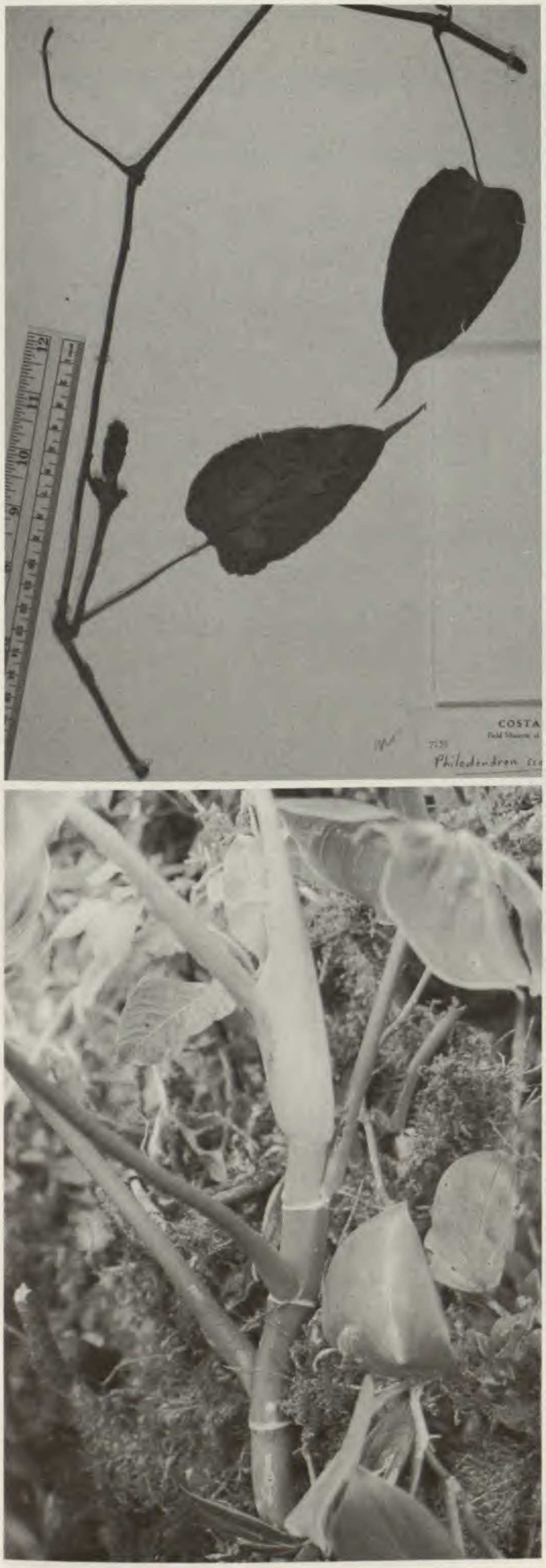


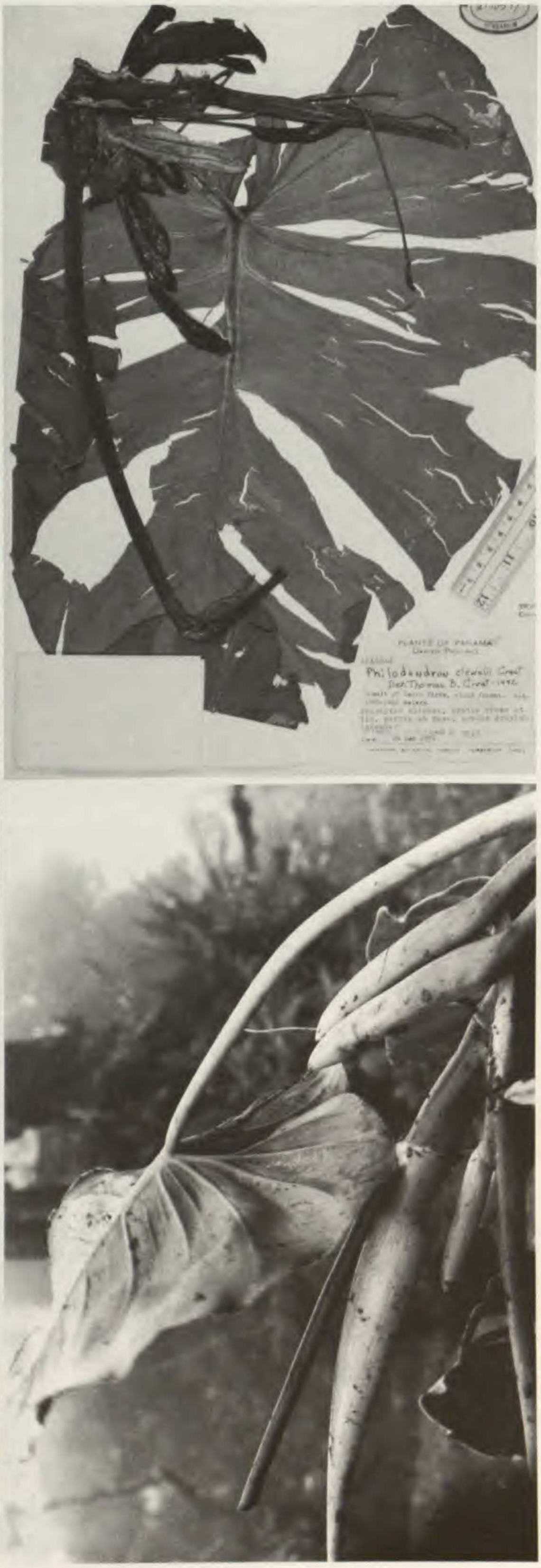


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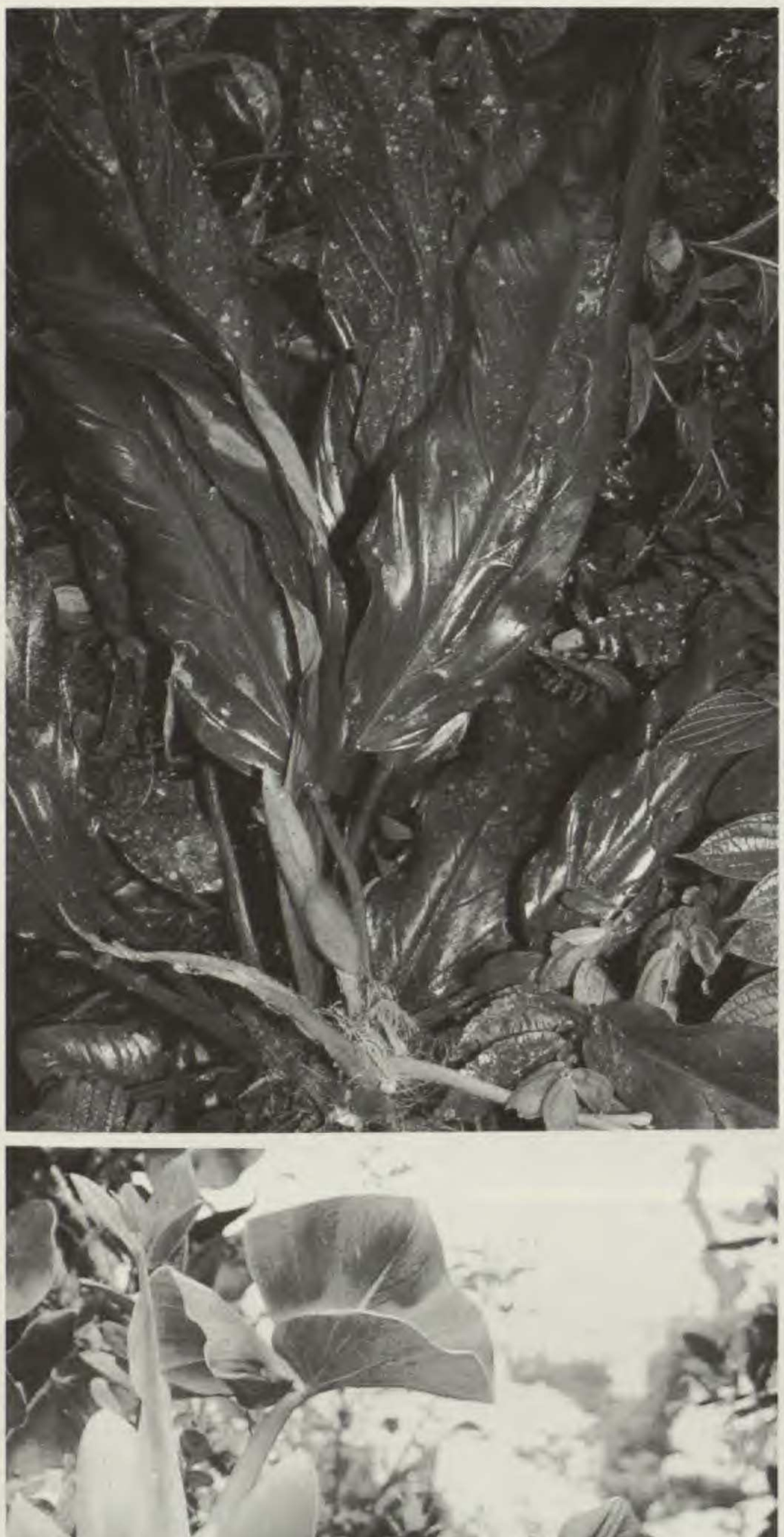








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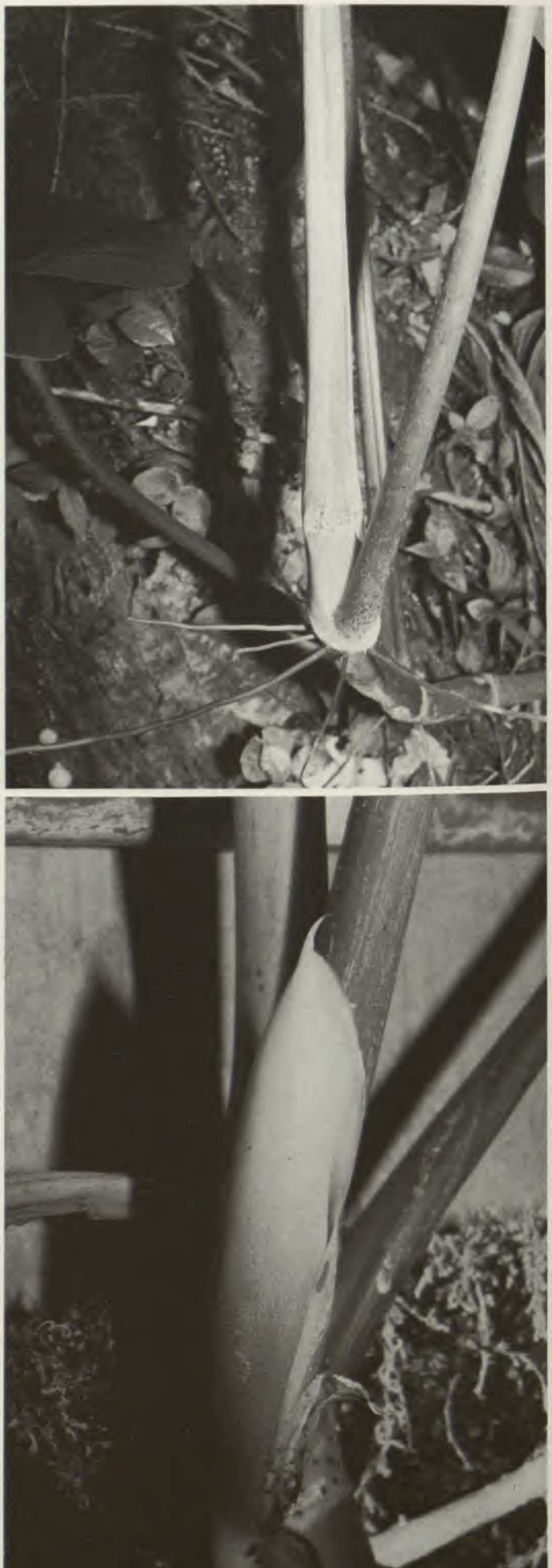






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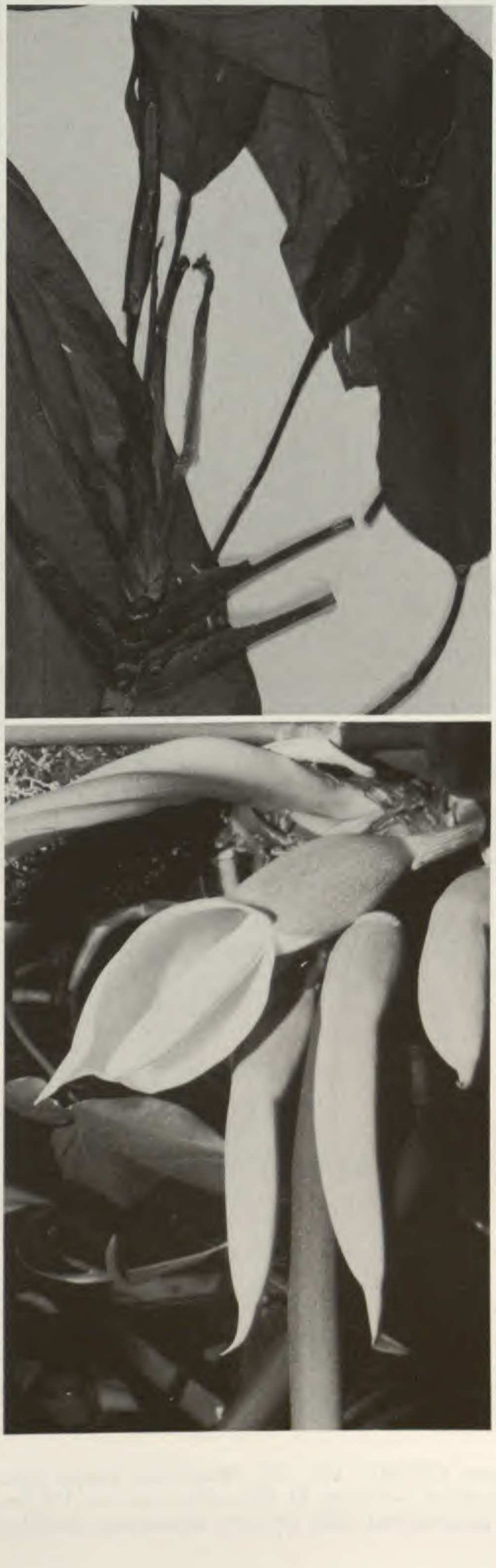






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Figures 185–188. —185 (top L). *Philodendron ferrugineum*, cluster of inflorescences with one cut open (*Croat 25098*). 186–188. *P. fragrantissimum*. 186, 187 (top R & bottom L). (*Granville 5975*) Cultivated at the University of Utrecht Botanical Garden. —188 (bottom R). Habit with leaves with D-shaped petioles and inflorescences emerging from cataphylls (*Croat 11526*).









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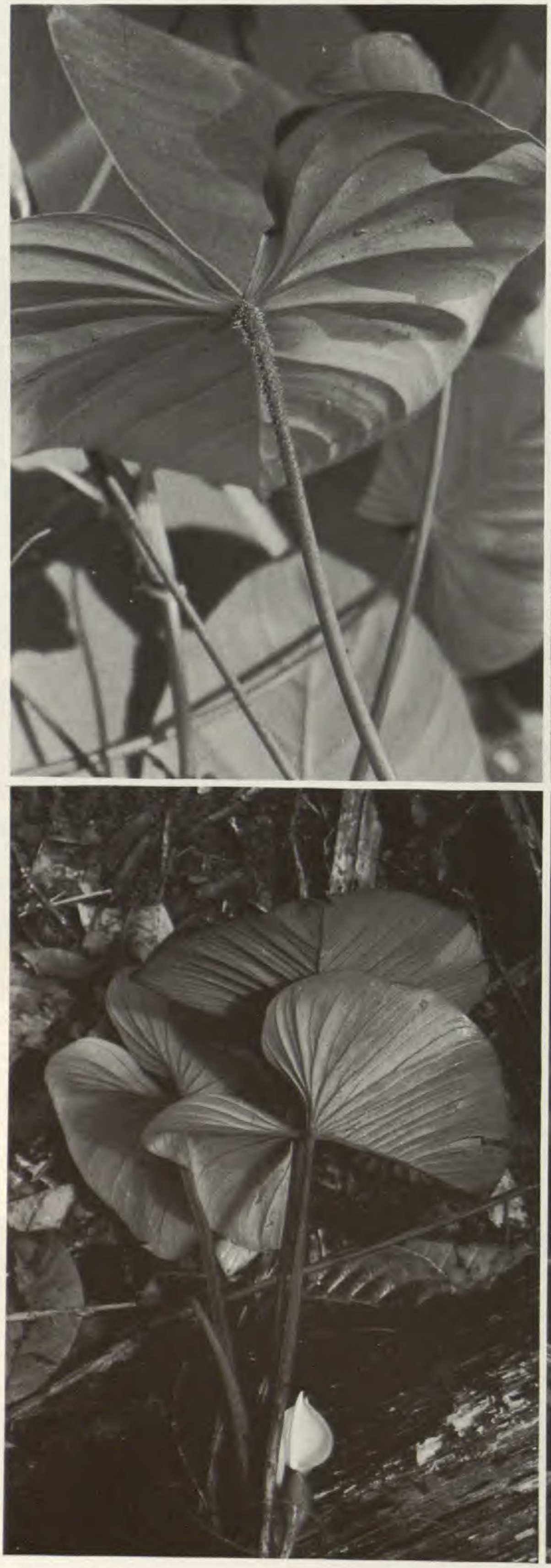




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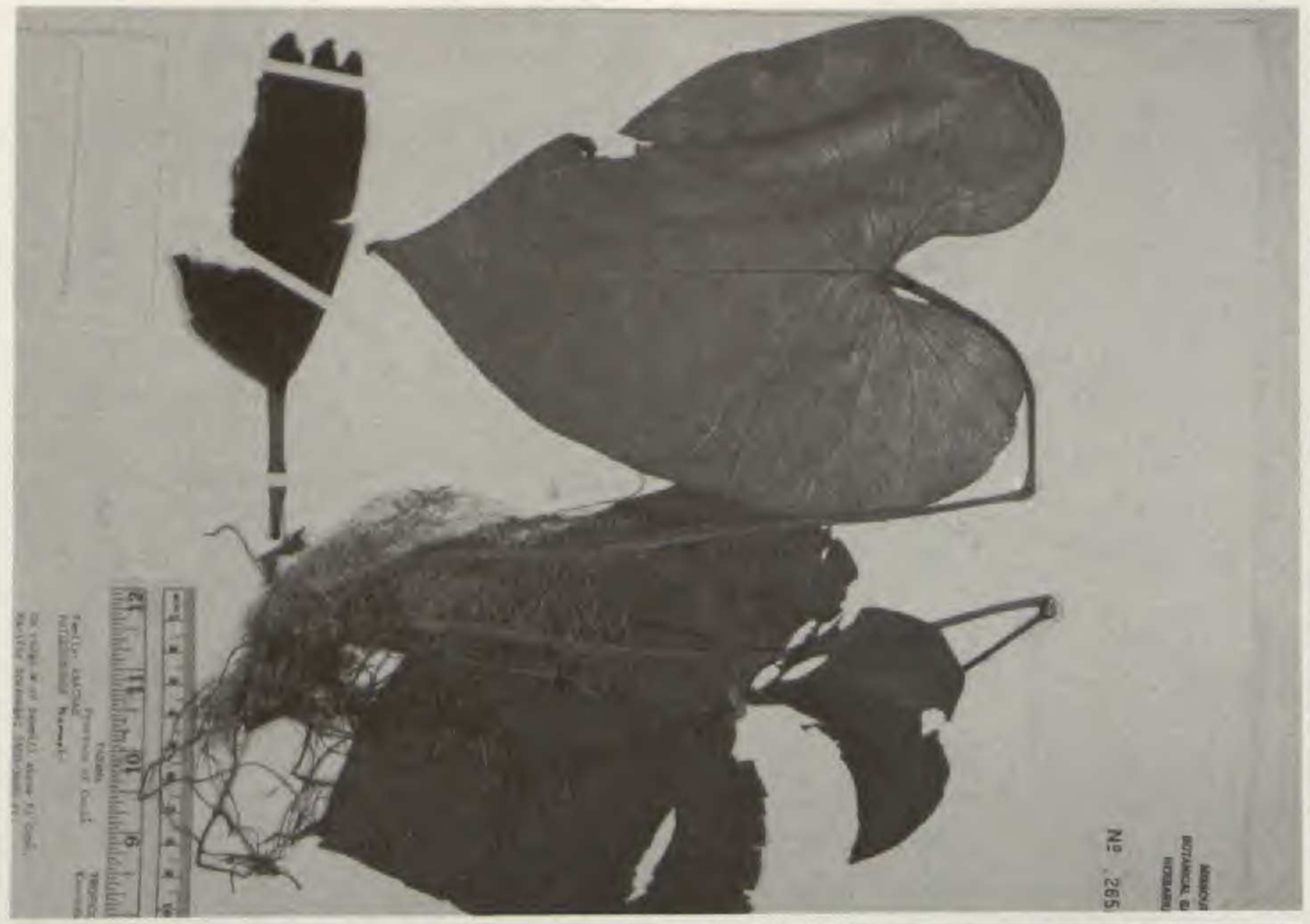






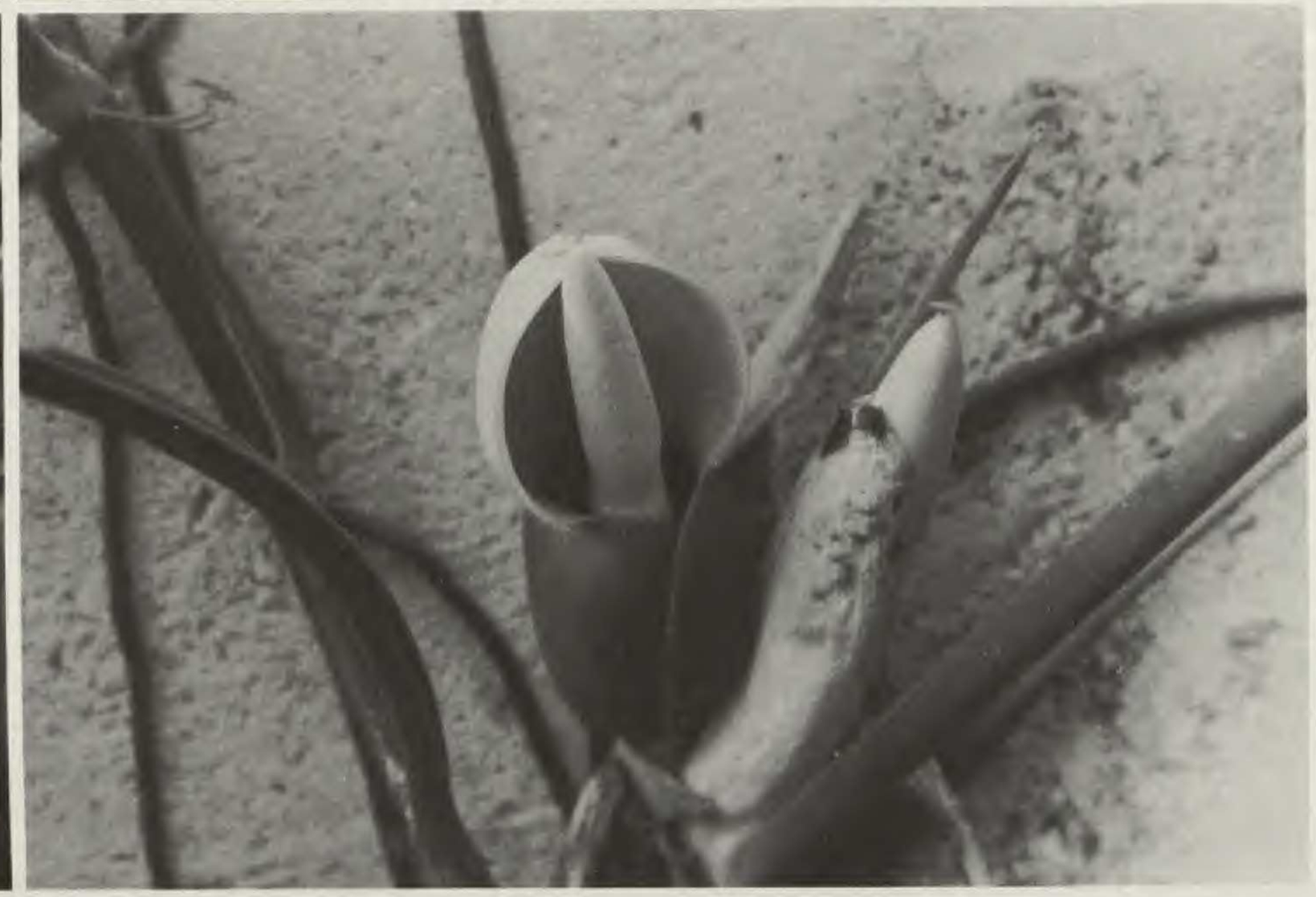


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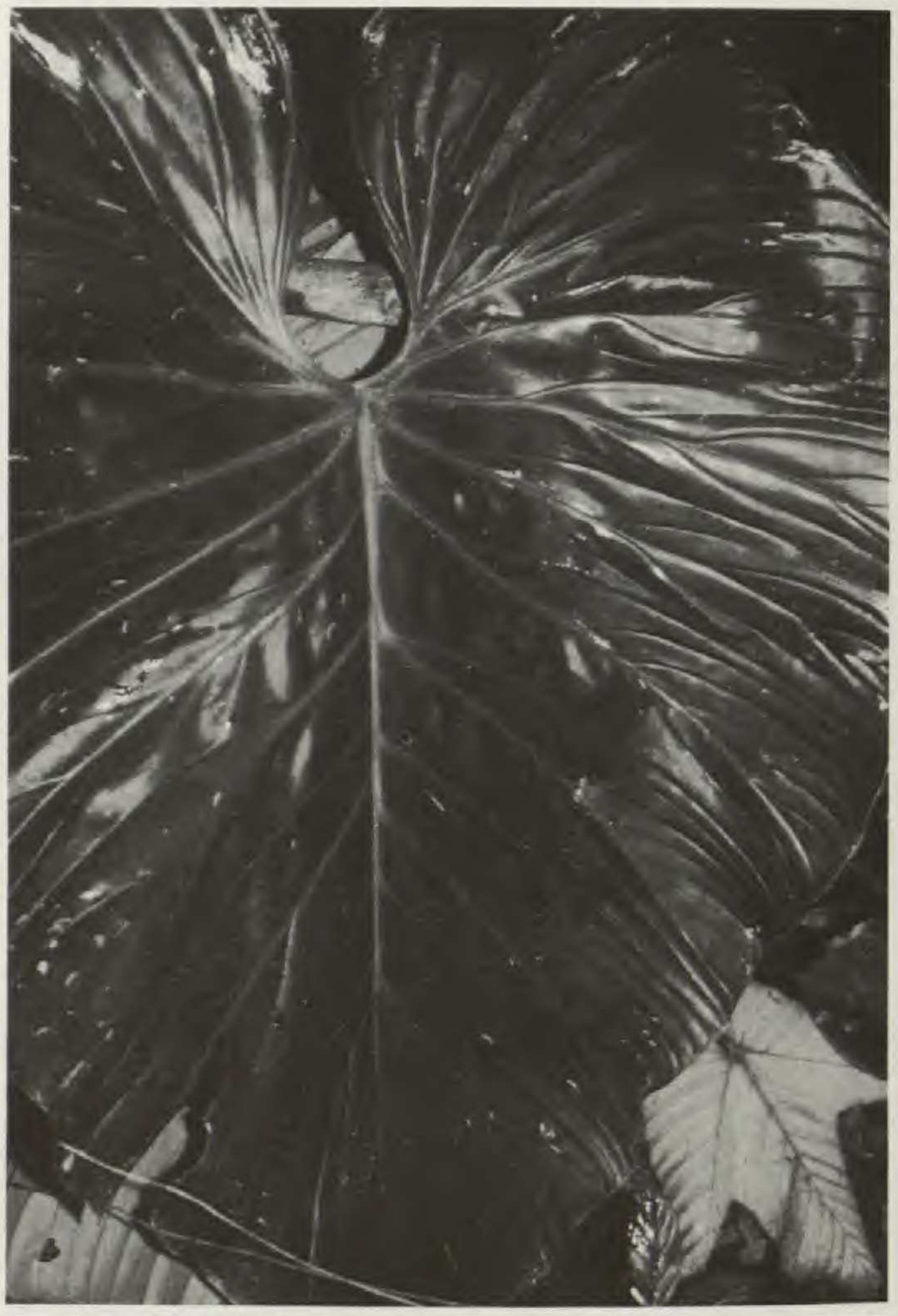






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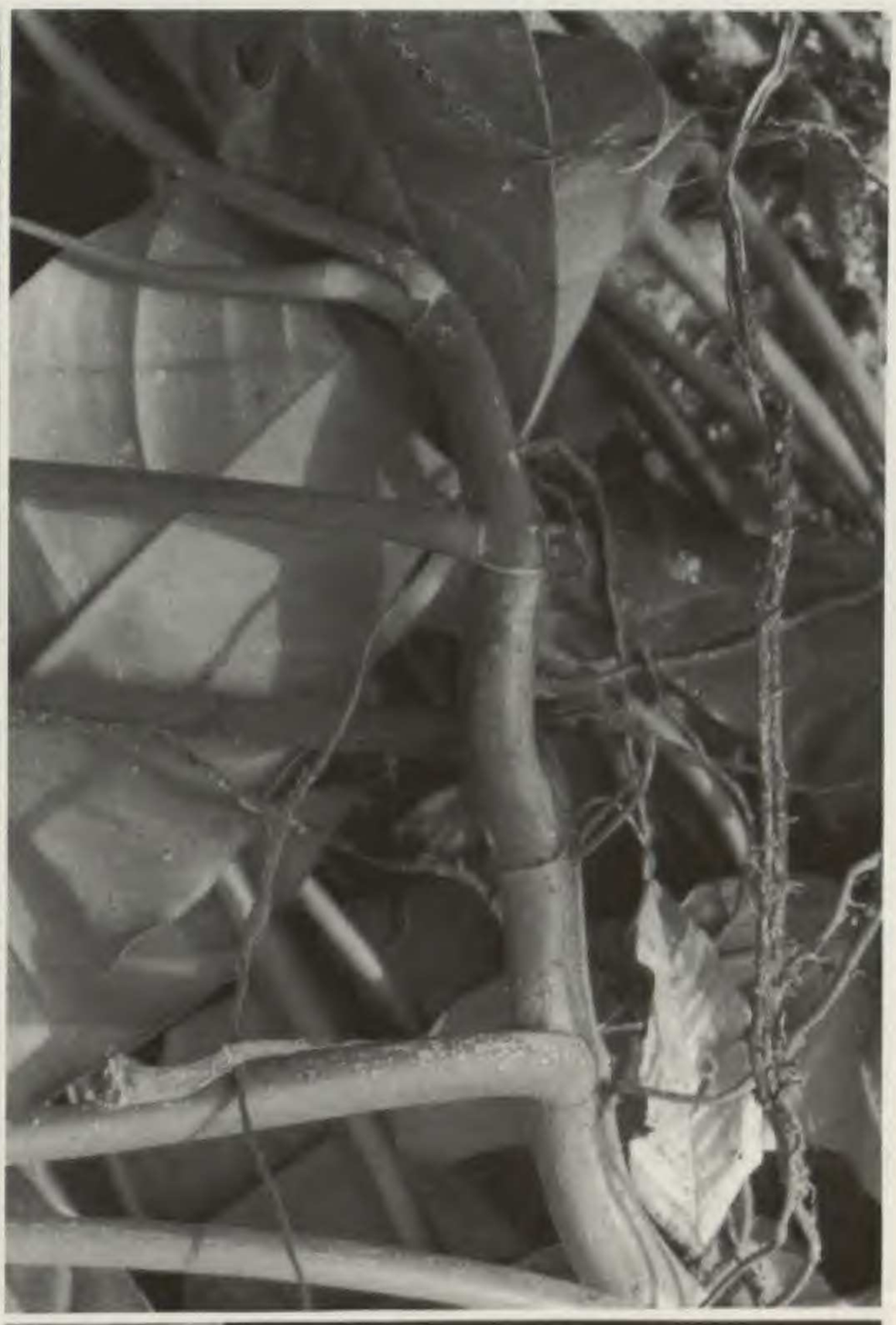
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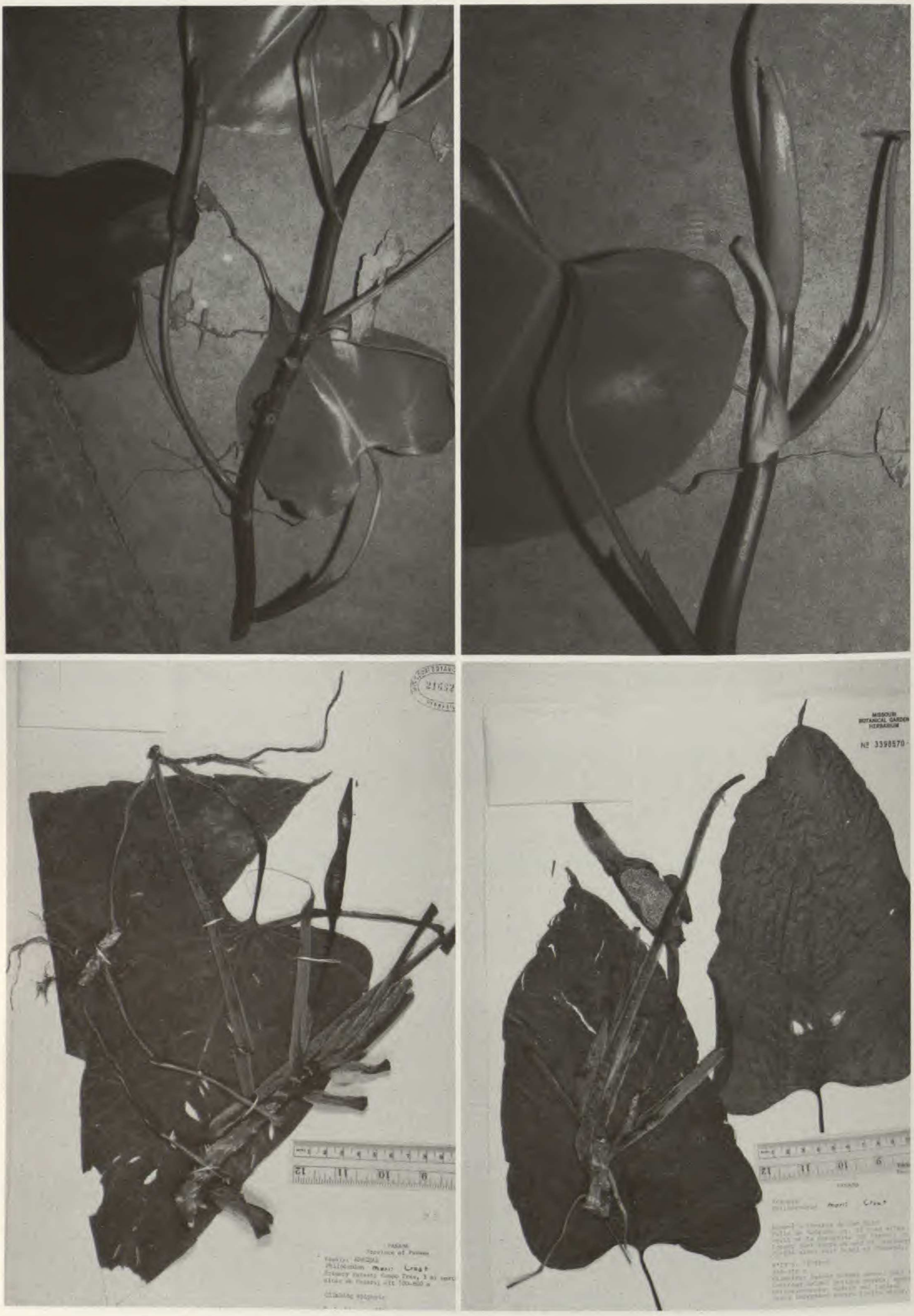
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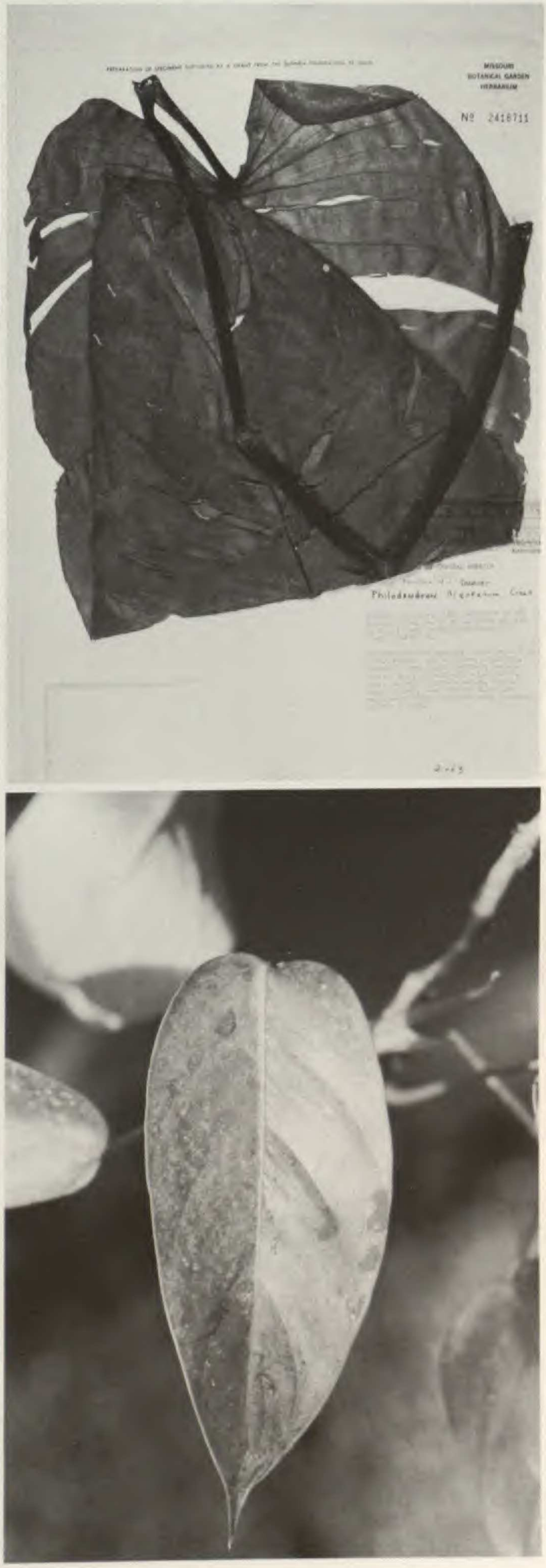


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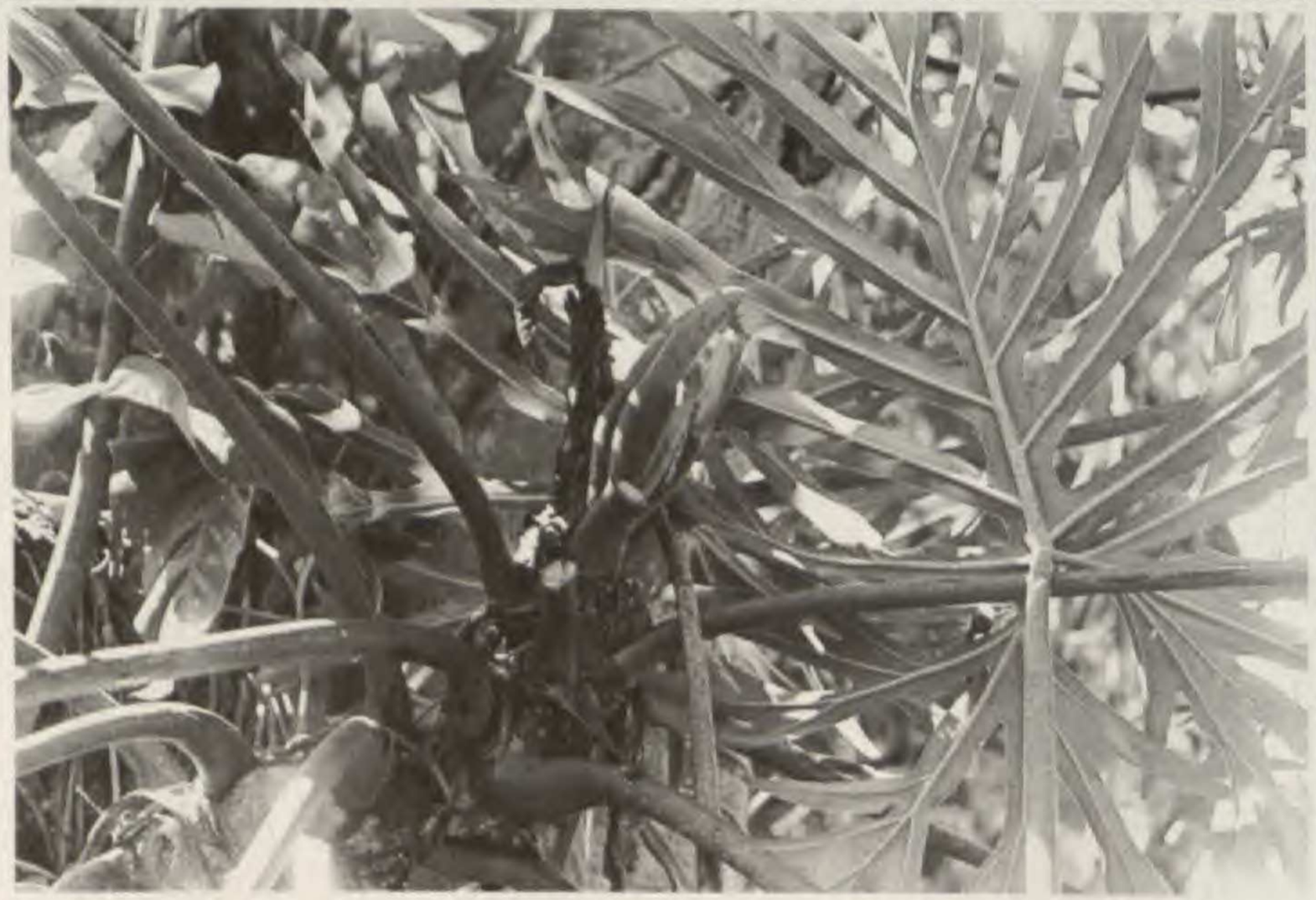




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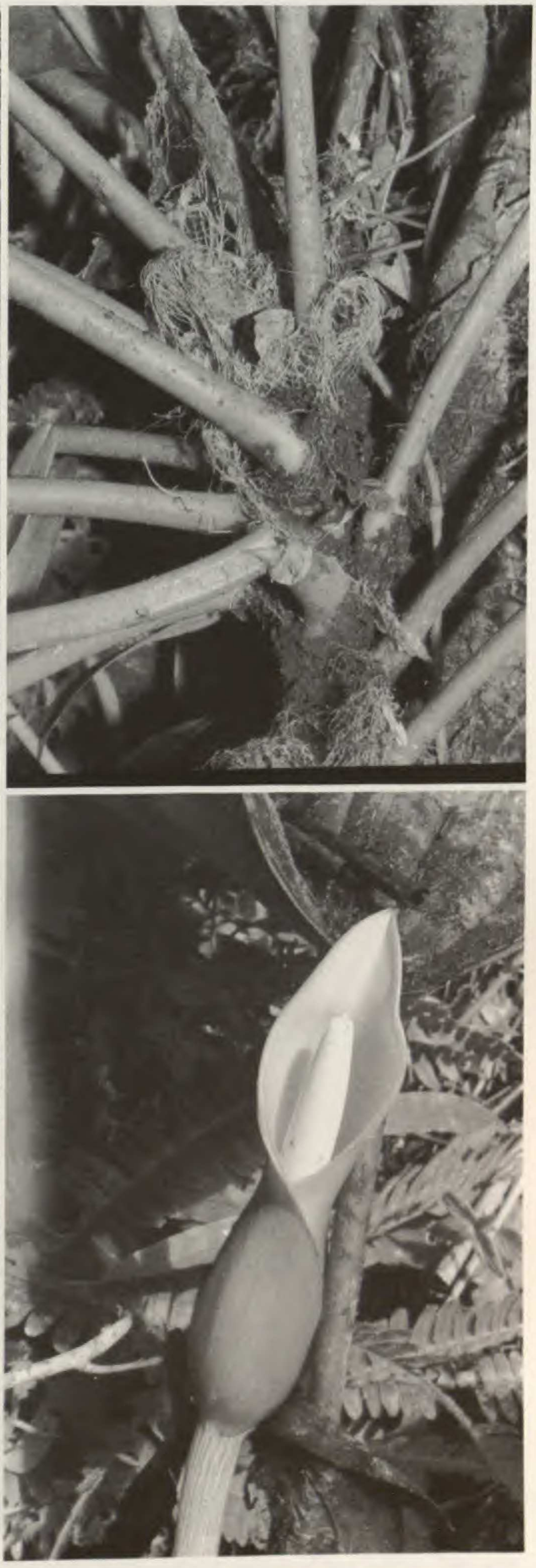




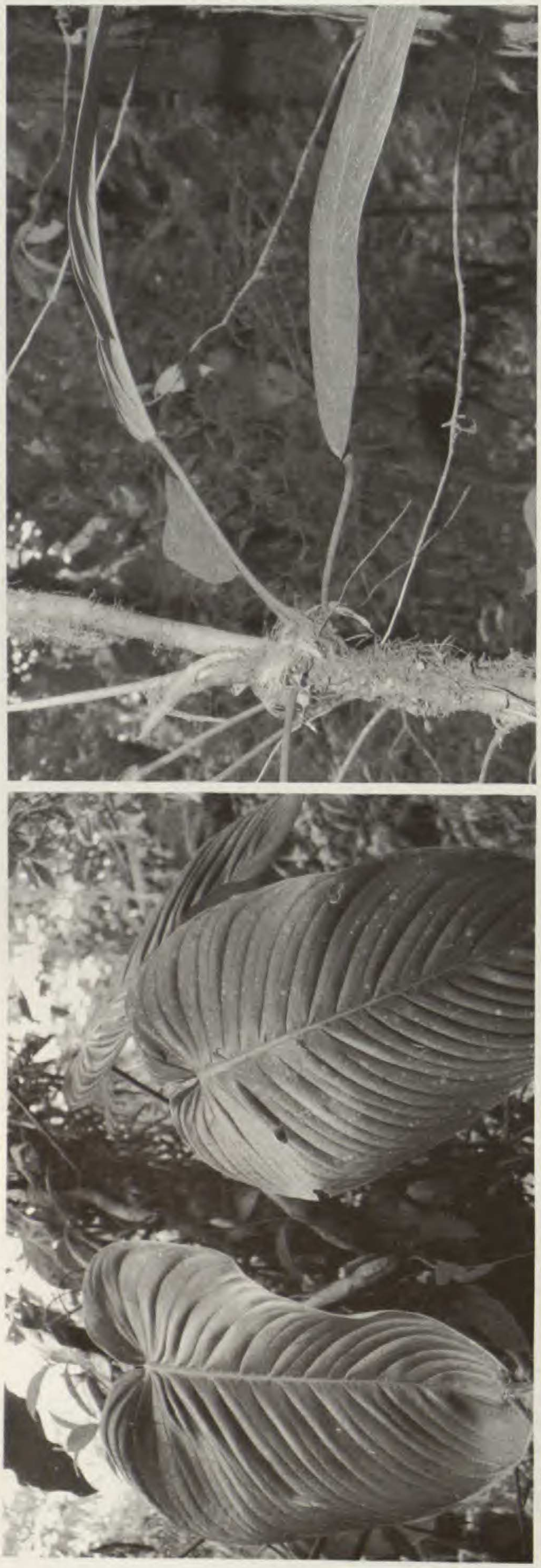


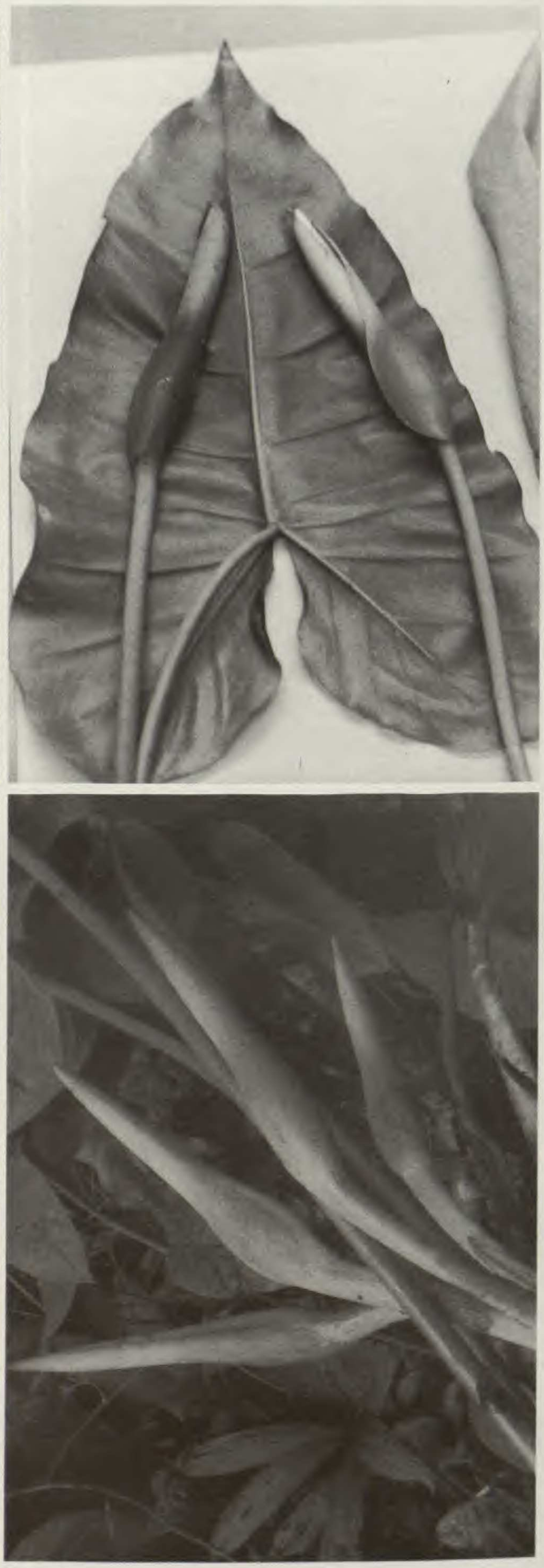
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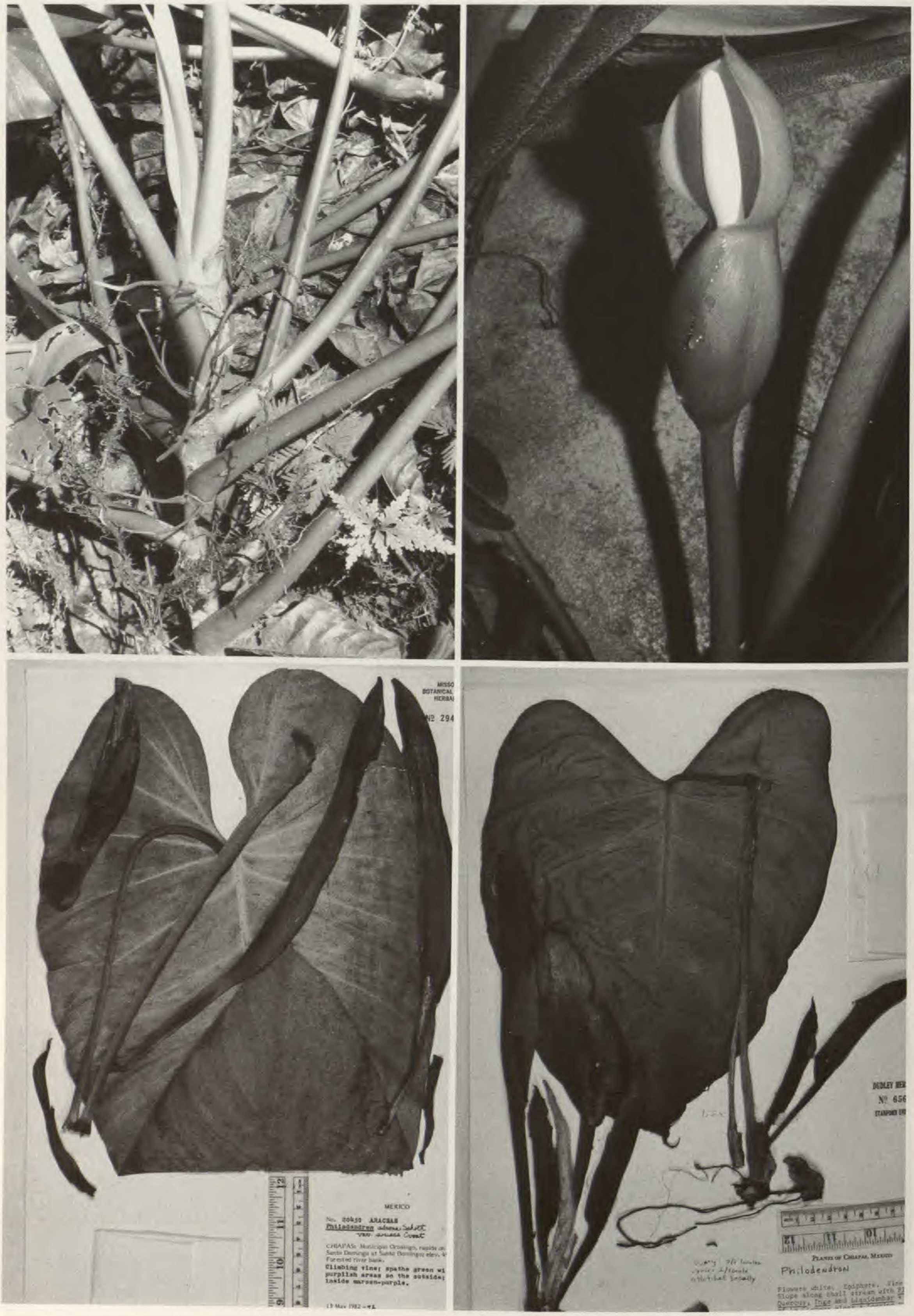


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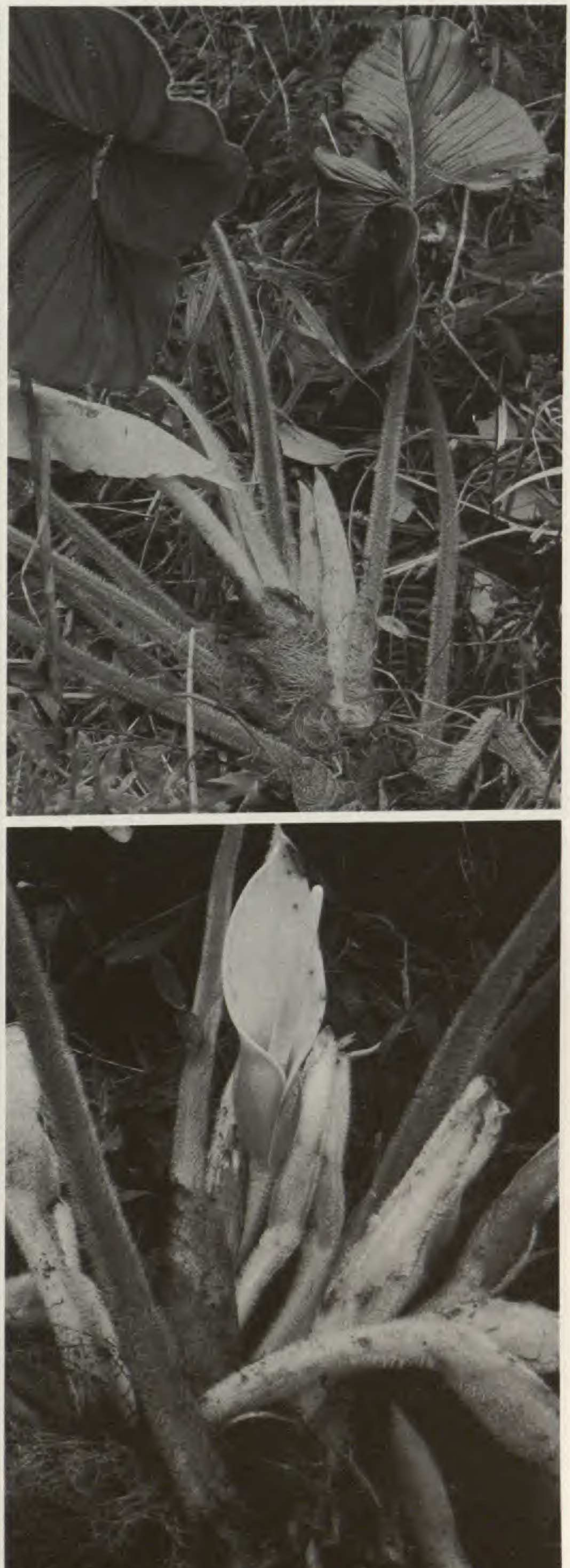


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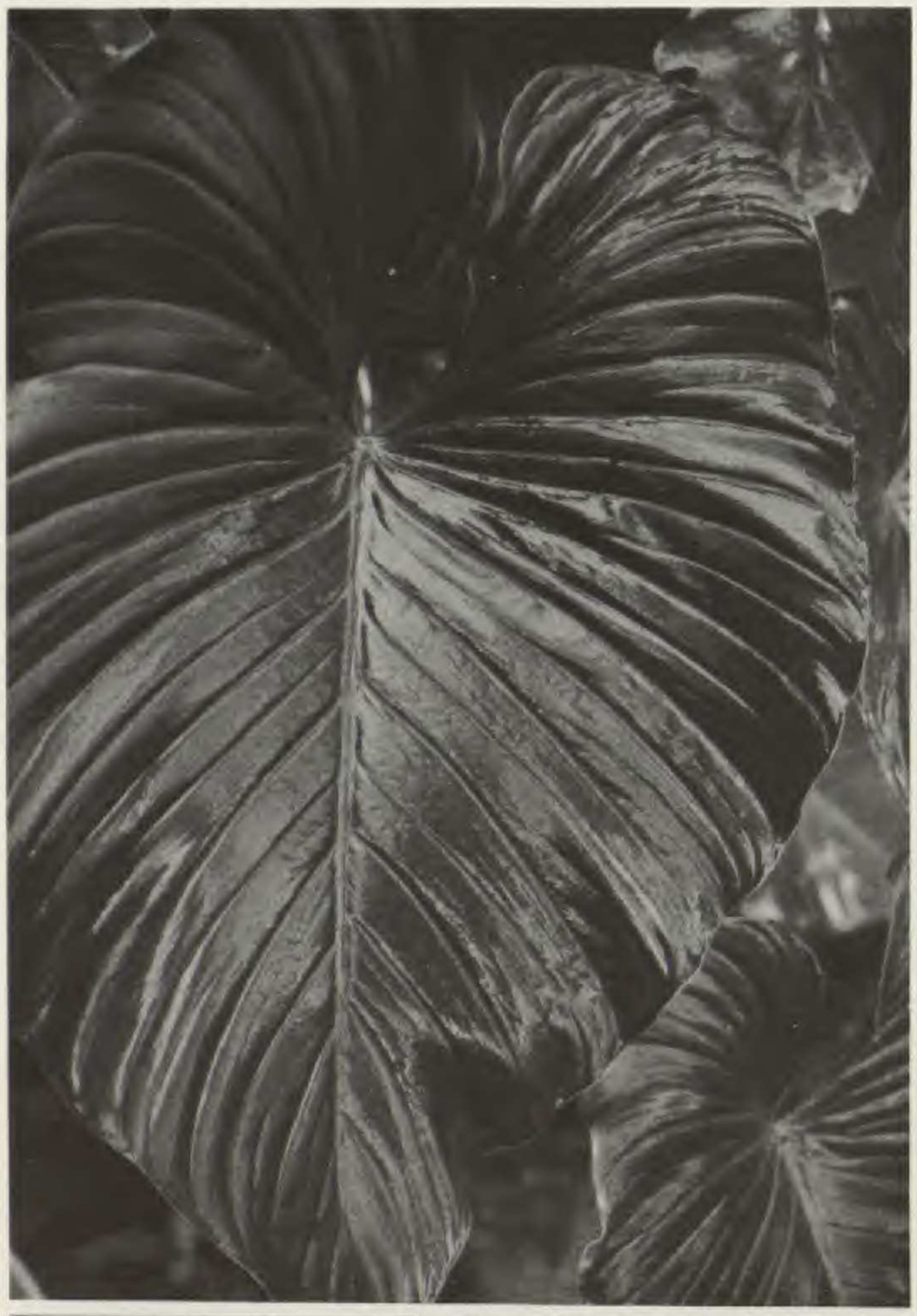




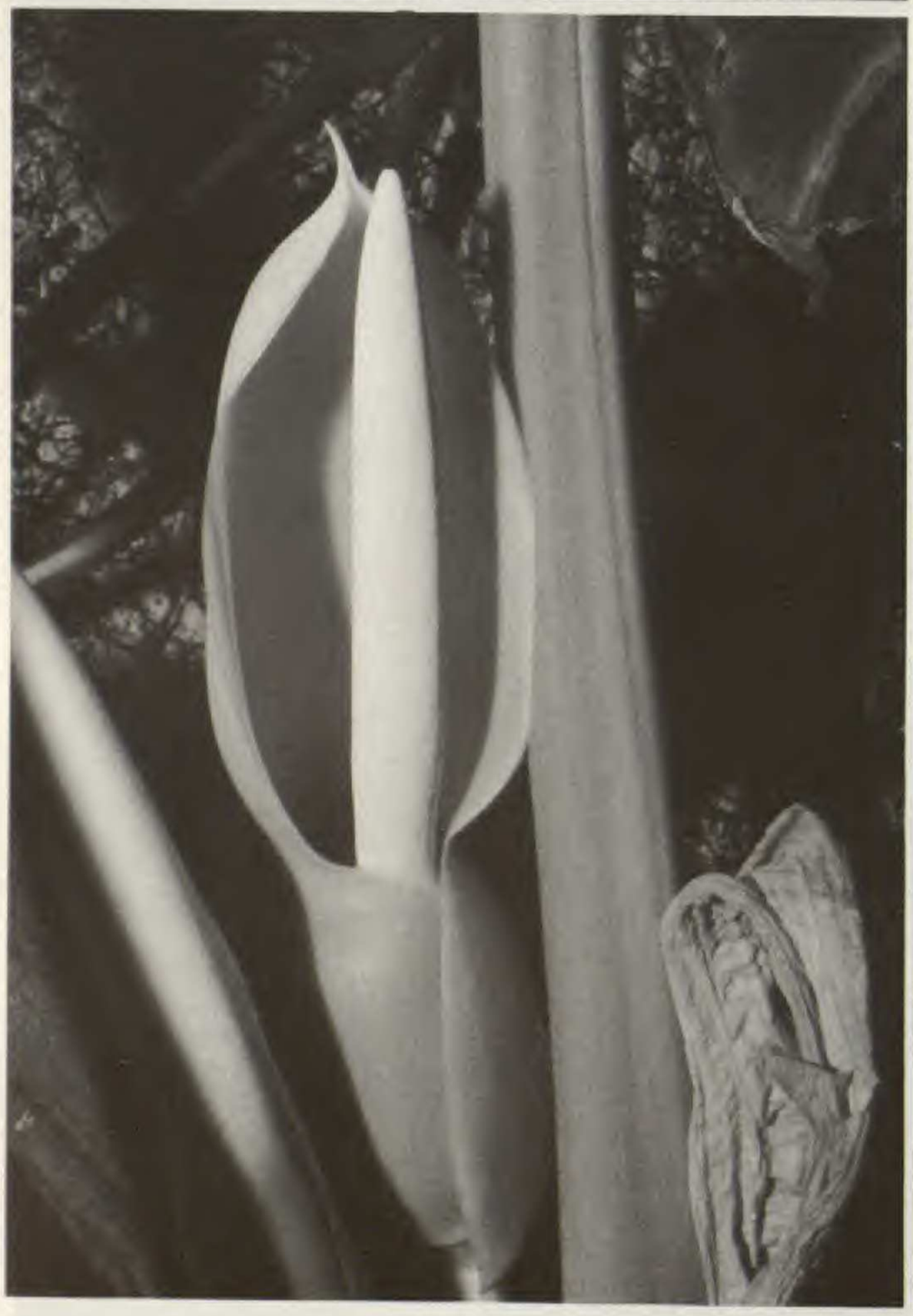




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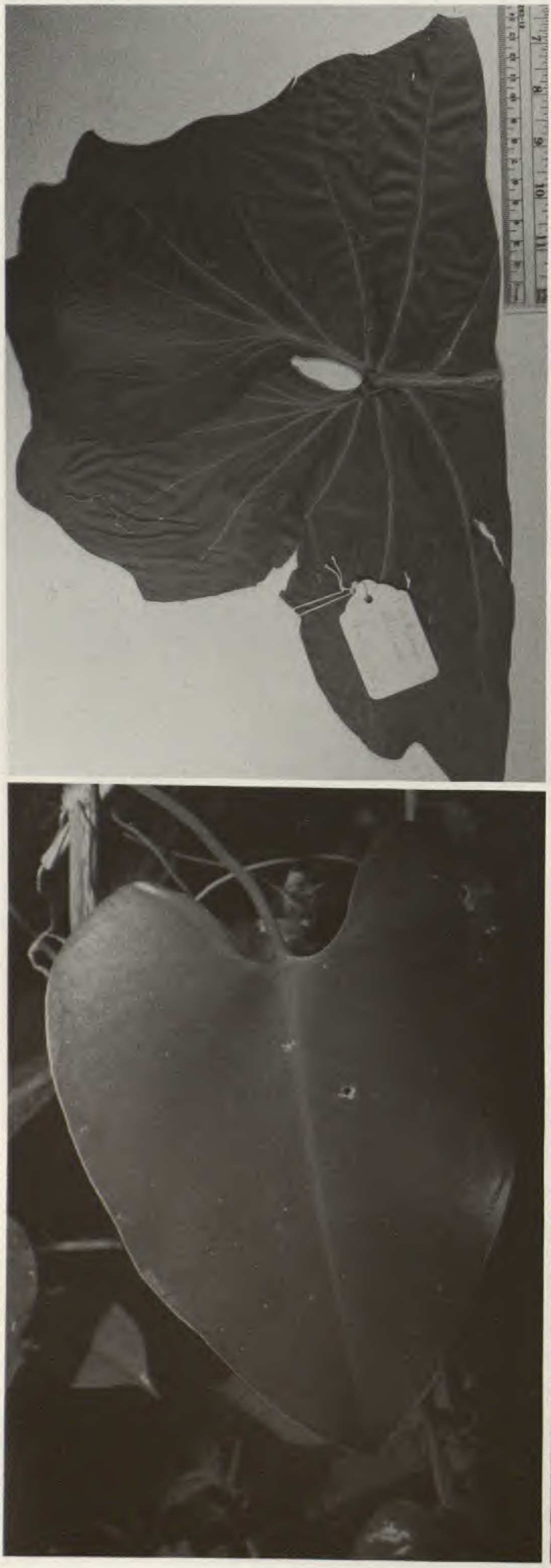




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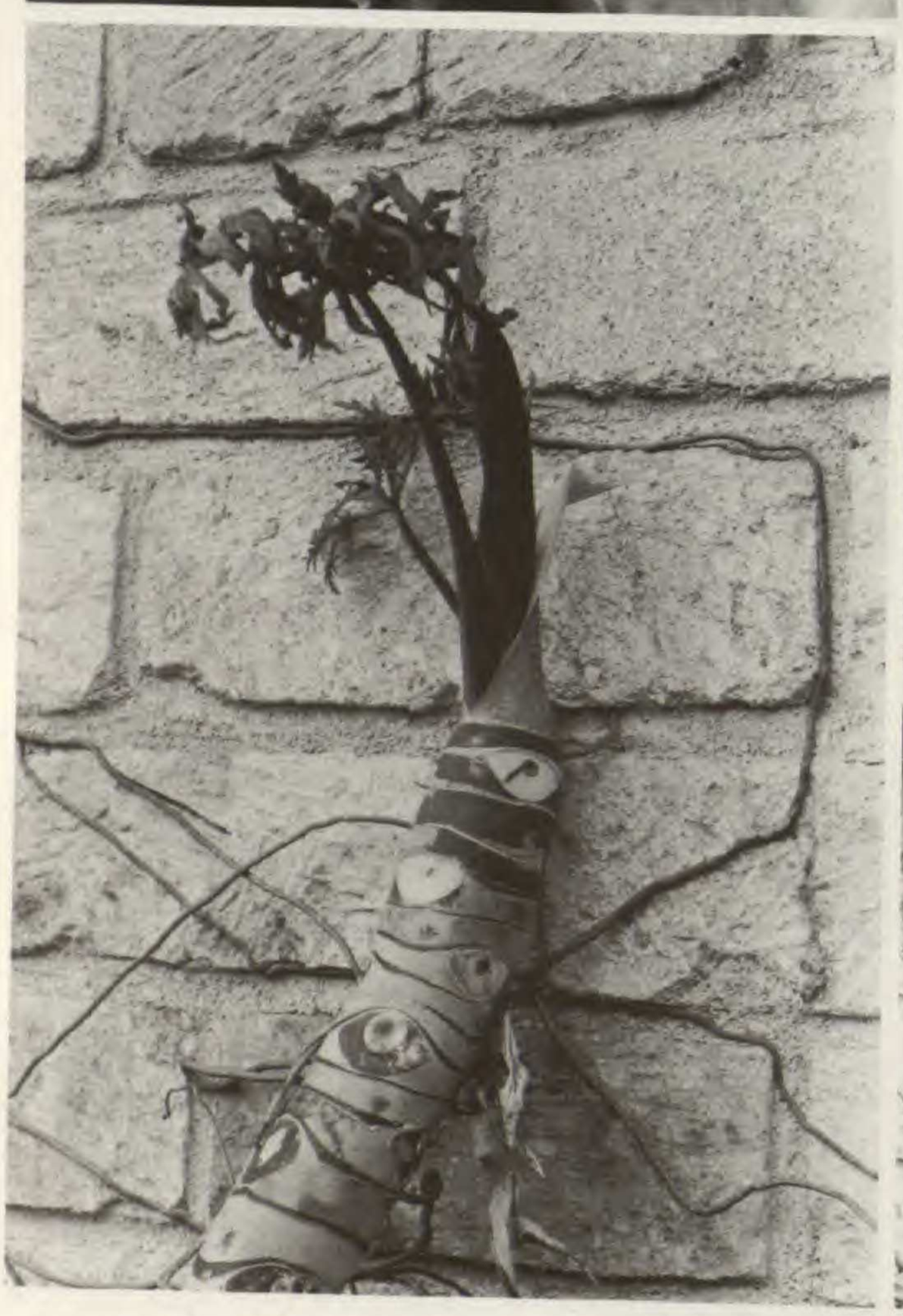




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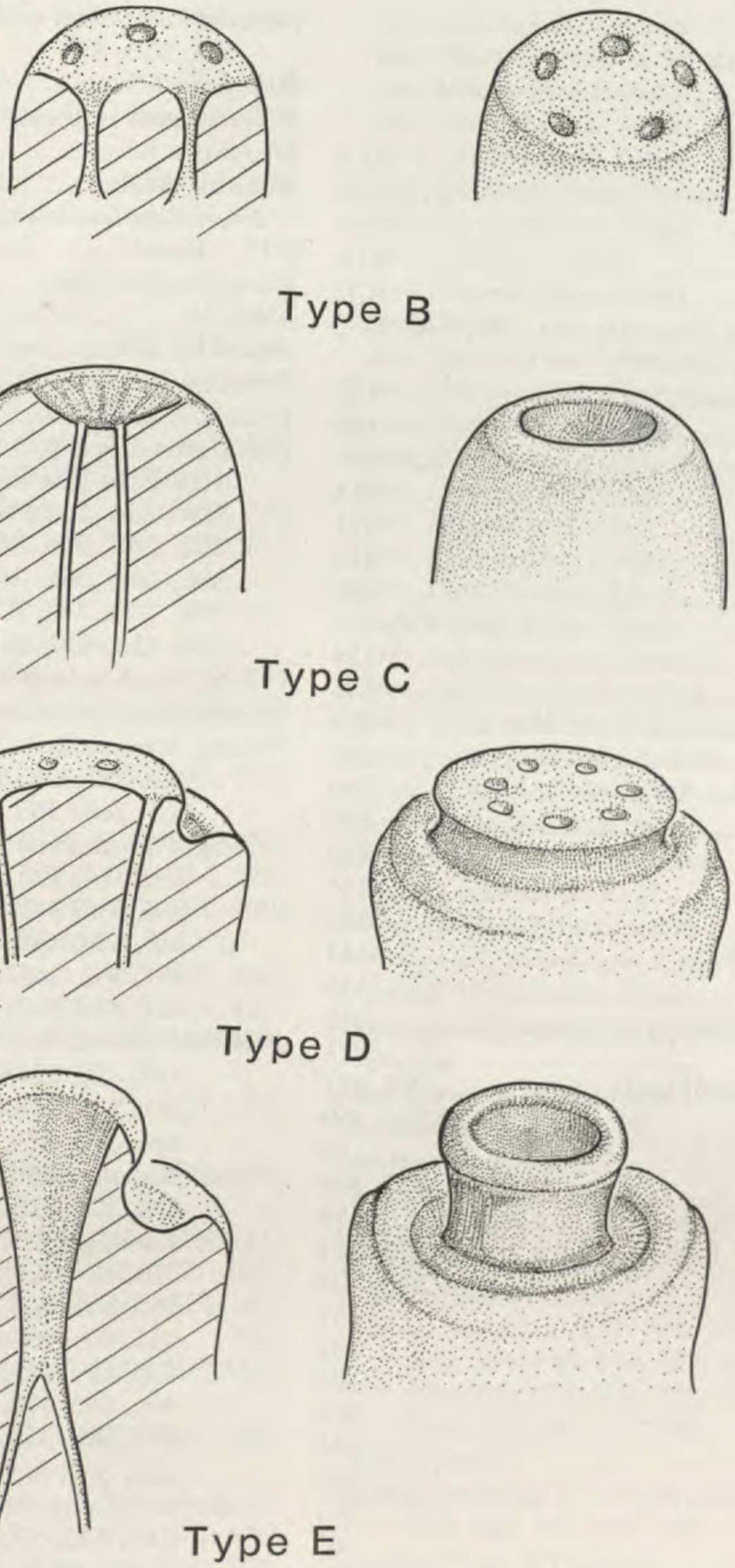


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A REVISION OF *STYRAX* (STYRACACEAE) FOR WESTERN TEXAS, MEXICO, AND MESOAMERICA[1]

Peter W. Fritsch[2]

ABSTRACT

Despite a recent taxonomic treatment of *Styrax* from North America and the Caribbean, the taxonomy of this genus has remained poorly understood. In an effort to clarify the taxonomy of *Styrax* from western Texas through Mesoamerica, morphological characteristics of over 2500 specimens from 29 herbaria were examined. The previous treatment emphasized vegetative characters for circumscription, whereas the present revision includes heretofore poorly characterized features of the androecium. This revision comprises 19 species and 24 taxa in the area considered, nearly three times as many species as recognized previously. It includes six new species (*S. gentryi, S. incarnatus, S. nicaraguensis, S. radians, S. steyermarkii, S. tuxtlensis*), two new subspecies (*S. platanifolius* subsp. *mollis, S. nicaraguensis* subsp. *ellipsoidalis*), three new combinations (*S. platanifolius* subsp. *stellatus, S. platanifolius* subsp. *texanus, S. platanifolius* subsp. *youngiae*), and two new species names (*S. austromexicanus, S. lanceolatus*). Two names (*S. glabrescens* var. *pilosus* and *S. jaliscanus*) are lectotypified. Nearly 70% of the species recognized in the revision are narrow endemics. This work has provided the basis for a taxonomic revision of all neotropical *Styrax* that is currently under way.

The genus *Styrax* comprises about 120 species of trees and shrubs distributed in eastern and southeastern Asia, the New World, and the Mediterranean region. It is a member of the family Styracaceae (12 genera, about 150 species), which, along with the Ebenaceae, Lissocarpaceae, Sapotaceae, and, according to some authors, the Symplocaceae, comprise the order Ebenales (Cronquist, 1981; Dahlgren, 1980; Takhtajan, 1980, 1987; Thorne, 1992). A phylogenetic analysis of the Ebenales based on chloroplast DNA *rbc*L sequences (Morton et al., 1997) tentatively indicates that Styracaceae are diphyletic, with *Styrax* sister to *Clethra* (of the monotypic Clethraceae). *Styrax* has essentially a Laurasian Tertiary relict distribution (as defined in Tiffney, 1985) except for a large neotropical component and a single species that extends east of Wallace's Line to New Guinea and

[1] I thank the curators of the following herbaria, who kindly made specimens available: A, AAU, B, BH, BR, CAS, CHAPA (one specimen), CR, DS, DUKE, F, GH, HCIB, IBUG, INB, K, LL, MEXU, MICH, MO, MSC, NY, POM, RSA, TEX, U, US, W, and WIS. I am indebted to Lisa K. Fritsch for help with the collection database, Porter P. Lowry II, Paul S. Manos, Stephen A. Spongberg, and Robert L. Wilbur for helpful comments on the manuscript, and Lisa Bush for illustrations. This work was supported by a grant from the A. W. Mellon Foundation and Duke University.

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several islands of the South Pacific (Perkins, 1907; van Steenis, 1932; Fritsch, 1995). The genus is characterized by a campanulate, white or pink, usually 5-parted corolla with petals connate at the base, usually twice the number of stamens as petals, a 3-locular, superior ovary, a linear style, and a 1–3-seeded drupe, nut, or 3-valved capsule with a persistent calyx. Leaf arrangement is alternate, and the vesture consists of scales or stellate hairs.

Infrageneric Classification

Styrax is currently divided into section *Foveolaria* (Ruiz & Pav.) Perkins, comprising taxa with 3- to 5-ovulate gynoecia (two species, Cuba and Peru), and section *Styrax*, with 16- to 24-ovulate gynoecia (all the remaining species; Perkins, 1907). Perkins (1907) maintained two series within section *Styrax*: series *Imbricatae* Gürke (about 30 species) and series *Valvatae* Gürke (about 90 species). As the names suggest, the species of series *Imbricatae* possess imbricate corolla aestivation, and those of series *Valvatae* possess valvate corolla aestivation. However, some species of section *Valvatae* are variable for aestivation type—sometimes even within the same individual (Perkins, 1907). For this reason van Steenis (1932) suggested that the two series are not "natural" (i.e., monophyletic) but offered no alternative classification. A recent study of the internal transcribed spacer regions of nuclear ribosomal DNA (Fritsch, 1995, 1996a) has supported the non-monophyly of the two series, but because of limited sampling in this study, the development of a revised classification at this time is premature.

Ongoing morphological studies of *Styrax* (Fritsch, unpublished data) suggest that characters in addition to corolla aestivation are important in the delimitation of infrageneric categories. The 60 or so neotropical evergreen *Styrax* species possess a drupe, although the fruit is nearly always mistakenly described in the literature as dry, hard-walled, and rugose because of the appearance of immature fruits on herbarium specimens (the mature fruit is rarely collected). The rest of the genus has dry fruits: in the paleotropical evergreen taxa they are thick-walled and either indehiscent or dehiscent via three valves; in the deciduous taxa of the northern subtropical and north-temperate zones they are thin-walled and usually dehiscent via three valves (rarely they are indehiscent). Corolla aestivation is valvate in all neotropical and paleotropical evergreen species, but valvate and/or imbricate in the deciduous species (Fritsch, 1995). On the basis of these characters, the delimitation of neotropical evergreen, paleotropical evergreen, and deciduous groups within *Styrax* appears to be justified. Additional phylogenetic work in the genus using both morphological and molecular characters is needed to lay the groundwork for a revised infrageneric classification.

Prior Work on Mesoamerican *Styrax* and Present Objectives

The present taxonomic revision was undertaken in conjunction with a treatment of Styracaceae in the ongoing series *Flora Mesoamericana*. There are two modern (20th century) treatments of *Styrax* in Mesoamerica (the region east of the Isthmus of Tehuantepec south through Panama) for use as reference works for the *Flora Mesoamericana* treatment. The first (Perkins, 1907) provided a treatment of the species of the region as part of a worldwide monograph of the Styracaceae and is the most recent worldwide treatment of *Styrax* to date. Perkins (1907) recognized six species from the region: *S. argenteus*, *S. conterminus*, *S. glabrescens*, *S. polyanthus*, *S. polyneurus*, and *S. warscewiczii*. The second (Gonsoulin, 1974) comprised part of a revision of North American, Central American, and Caribbean *Styrax*. In this treatment, the number of species in this region was reduced to three: *S. argenteus*, *S. conterminus*, and *S. glabrescens*. As a basis for this reduction, Gonsoulin (1974) argued (with some justification) that Perkins was a notorious splitter who disregarded continuous character variation. Gonsoulin (1974) also placed several new species that had been described subsequent to Perkins's (1907) monograph in synonymy under *S. argenteus*. Gonsoulin's revision, having been based on much more data than Perkins's, initially appeared to provide an adequate context for undertaking the *Flora Mesoamericana* treatment.

However, it became clear during early examination of Mesoamerican material that Gonsoulin (1974) had made a number of problematic taxonomic decisions, particularly concerning the circumscription of *S. argenteus*. This species was divided into three loosely defined varieties that encompassed all evergreen *Styrax* in Mexico and Mesoamerica except *S. conterminus*, which possesses an unusual trichome type easily delimiting it from the rest of the material examined by Gonsoulin. He justified this circumscription by comparing it with the variable nature of the characters used in Perkins's (1907) key to differentiate additional species, specifically pubescence on the lower laminar surface, flower length, and calyx length. I agree with Gonsoulin (1974) that these characters by themselves provide poor support for species cir-

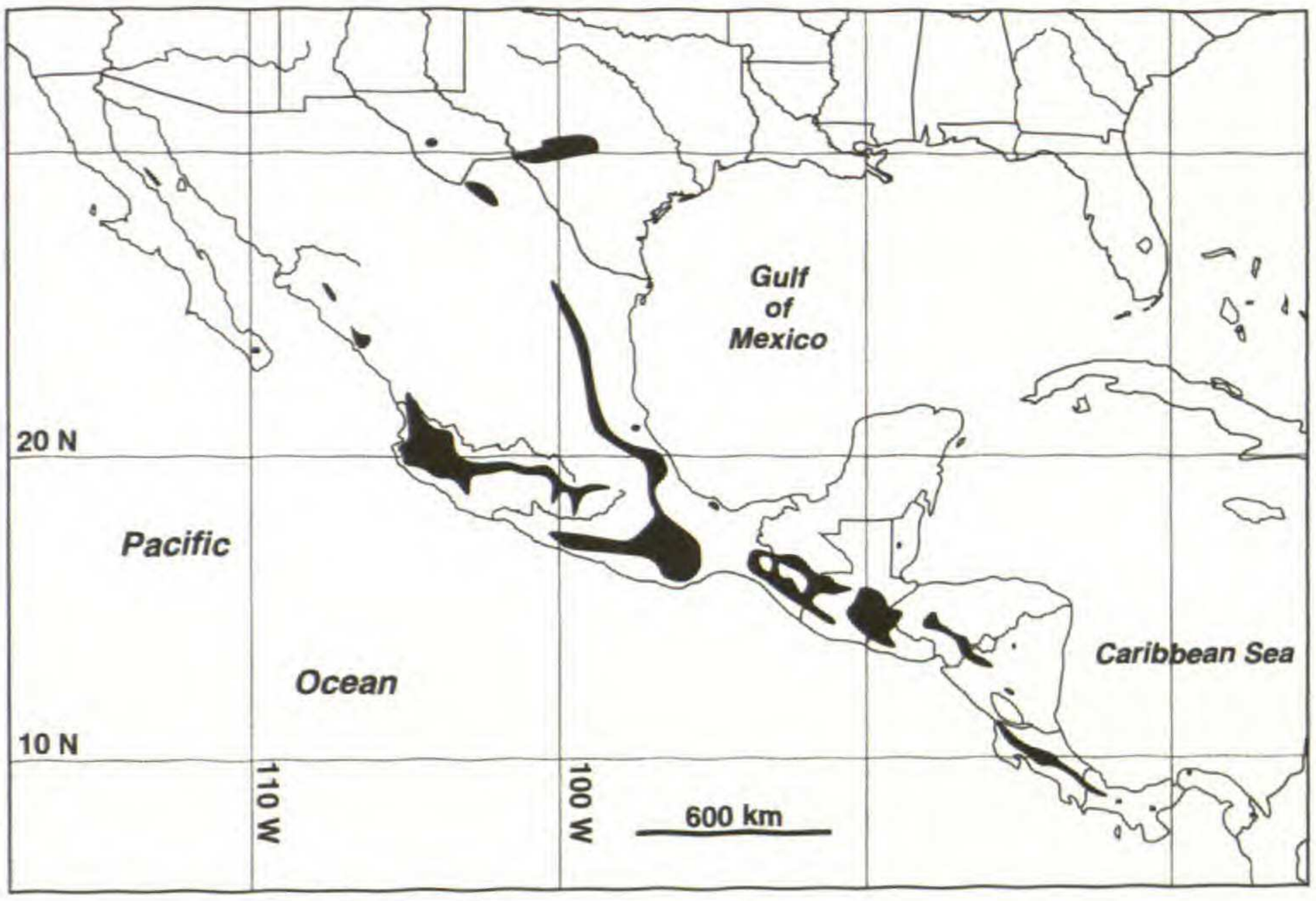


Figure 1. General distribution of *Styrax* in western Texas, Mexico, and Mesoamerica.

cumscription in *Styrax*, and it is unfortunate that Perkins provided only these characters in her key, because she included a number of critical androecial characters in her descriptions that at once distinguish *S. argenteus* from many of those taxa placed in synonymy by Gonsoulin. Apparently Gonsoulin surmised that, because she rarely included them in her key, Perkins considered androecial characters inconsequential. On this basis, he apparently decided not to pursue the potential utility of androecial characters for circumscription, for he did not employ them in the key to species or describe them to any significant degree.

The questionable concepts of circumscription in Gonsoulin (1974) were compounded by various nomenclatural and bibliographic errors in the same work, making the application of names to taxa I had recognized in the Mesoamerican region uncertain. Although Perkins's (1907) treatment was careful, I considered this work outdated and the species concepts within it too narrow for reliable use. Therefore, I decided to examine not only material from Mesoamerica, but also all *Styrax* material from western Texas and Mexico, as well as a limited amount of South American material, to provide the general context for a clear and unambiguous treatment for *Flora Mesoamericana*.

Geographic Distribution, Endemism, and Ecology

Styrax exhibits a somewhat discontinuous distribution in western Texas, Mexico, and Mesoamerica (Fig. 1). The northern half of the range can be divided into two parts. In the northeastern part of the region members of the genus occur from the Edwards Plateau and the Davis Mountains of Texas south along the Sierra Madre Oriental to Oaxaca; in the northwestern part they extend from the Cape Region of Baja California Sur and southern Sinaloa to Oaxaca along the western slope of the Sierra Madre Occidental, the southern slope of the trans-Mexican volcanic belt, and the Sierra Madre del Sur, bypassing the low elevations of the Río Balsas basin. Collections are also known from the Tuxtlas Range in Veracruz. The southern half of the range extends from the Sierra Madre and Central Plateau of Chiapas through the mountainous regions of Guatemala, northwestern El Salvador, and Honduras to a small portion of northern Nicaragua, and then along the Pacific slope of the cordillera from extreme southern Nicaragua to western Panama. Isolated localities have been recorded in Belize, central Nicaragua, and central and eastern Panama.

The 19 species of *Styrax* recognized in this treatment are all endemic to the region of interest except *S. glabratus* and *S. peruvianus*, both of which also occur in South America. Only six species are relatively widespread and fairly common: *S. argenteus*, *S. glabratus*, *S. glabrescens*, *S. radians*, *S. ramirezii*, and *S. warscewiczii*. Nearly all the rest are narrow endemics and are likely to be rare, vulnerable, endangered, or extinct (terms sensu Lucas & Synge, 1978). Two species are known with certainty only from single collections (i.e., *S. tuxtlensis*, *S. panamensis*). *Styrax platanifolius* has a relatively large range but is uncommon; it comprises five subspecies, all of which are rare. In contrast, *S. magnus* occurs only from central Chiapas to southwest-

ern Guatemala yet has been collected many times; thus it is probably common within its narrow range, although it is unclear to what extent sampling artifact has affected the perceived abundance of this and other species. Locating additional populations of all narrow endemics, especially *S. gentryi*, *S. incarnatus*, *S. panamensis*, *S. steyermarkii*, and *S. tuxtlensis*, will be invaluable for comprehensive documentation of morphological features, biogeographic studies, and conservation.

Species of *Styrax* are found most often from 500 to 2500 m elevation. Several species (*S. argenteus*, *S. glabratus*, *S. panamensis*, *S. radians*) occur additionally or exclusively at elevations < 500 m; others (*S. austromexicanus*, *S. glabratus*, *S. ramirezii*, *S. warscewiczii*) extend to 3000 m elevation or more. According to herbarium specimen information, the genus is most often associated with *Quercus* and *Pinus* but can occur in a wide variety of forested situations, such as tropical humid forests, subtropical deciduous forests, seasonal evergreen forests, temperate deciduous forests, coffee plantations, and open savannas. *Styrax platanifolius* subsp. *youngiae* grows in woodlands composed of *Acer*, *Arbutus*, *Cercis*, *Juniperus*, and *Quercus* (*Wendt 582*), and also those composed of *Pinus* (piñon) and *Juniperus* (*Johnston et al. 11888*). Many species show a distinct preference for mesic microhabitats, such as canyons, draws, and other riparian situations. However, individuals of various *Styrax* species are also found in less protected situations, such as pastures and wind-swept ledges. Within primary forests, the tree species (i.e., all except *S. jaliscanus* and *S. platanifolius*) are usually understory or mid-canopy trees, seldom attaining a height of > 20 m. They also occur in secondary forests and other disturbed situations such as roadsides, burned-over areas, plantations, and open fields.

Locating populations of *Styrax* species in the field using herbarium label information can be difficult, primarily because they generally are local, sporadic, and normally small (< 30 individuals). Furthermore, members of the genus lack easily observable diagnostic features that would otherwise facilitate identification at a distance. The smooth or cracked gray bark and alternate, simple leaves with entire margins typical of the evergreen members of the genus are similar to many associates, e.g., *Ocotea* of the Lauraceae.

The deciduous species of *Styrax* generally flower in April and May and produce mature fruit by September; however, at low latitude they appear to possess a broader range of flowering and fruiting times. In contrast, the evergreen species flower and fruit at variable times throughout the year. The factors controlling flowering times are unknown. The fruits in the deciduous group (and likely in the evergreen group) take several months to mature; in the evergreen group, maturation from the green, relatively hard phase of fruit development to the purplish black, fleshy mature phase is not synchronous within an infructescence, and change of single fruits to the fleshy phase likely occurs quickly (within days).

Some neotropical species (*S. argenteus*, *S. glabratus*, *S. nicaraguensis*, *S. panamensis*, and *S. steyermarkii* in the present treatment) bear relatively long and stiff, stellate hairs that form a dense mass on the ventral side of the distinct portion of each stamen filament (Figs. 11, 12). The arms of the hairs are predominantly oriented along the longitudinal axis of the flower. A high proportion of the arms belonging to hairs nearest the distal end of the filament point upward; these are usually the longest in the hair mass (0.8–2 mm long). In the same location on each filament, two longitudinally oriented auricles can occur (*S. argenteus*, *S. nicaraguensis*, *S. peruvianus*, and *S. steyermarkii* in the present treatment; Figs. 12, 13). They are usually obscured by the dense hair mass that surrounds them; in *S. peruvianus* the trichome arms (in this case, scales) are relatively short and the auricles are larger and more prominent than those of the other species in the treatment (Fig. 13). The dense hairs and auricles occupy much of the space within the stamen tube and partially cover the ovary. The auriculate and densely pubescent conditions are both probably derived within *Styrax*: the genus *Pamphilia* Mart., likely the sister group to *Styrax*, lacks auricles and pubescence. In the floral bud stage, the auricles and/or pubescence occupy the cavity between the basal end of the anther and the apex of the ovary, and therefore may help to protect the bud from small herbivores.

In all other species of *Styrax* treated here, the ventral side of the distinct portion of the stamen filament lacks both auricles and a mass of stiff-armed stellate hairs, and the hairs nearest the distal end of the filaments are not noticeably longer nor do they have predominantly upward-pointing arms. The pubescence that is present is instead short-armed (to ± 0.7 mm long) and situated mainly along the filament margins (Fig. 10). The face of the filament proper (as opposed to the margin) is often glabrous proximally, becoming sparsely to densely pubescent distally.

Little comparative work has been done on the reproductive biology of *Styrax* species, especially those within the region of study. The most detailed analysis of breeding systems and pollination biology in the genus has been conducted by Sugden













Figures 2–7. SEM micrographs of the calyx vesture in various *Styrax* taxa from Mexico and Mesoamerica. —2. *Styrax argenteus, Breedlove 28487* (DS). —3. Stellate form of *Styrax ramirezii, McVaugh 11766* (MICH). —4. Small-scaled form of *Styrax ramirezii, Koch & Sánchez 7929* (MO). —5. *Styrax warscewiczii, Breedlove & Thorne 30989* (DS). —6. *Styrax steyermarkii, Steyermark 48666* (F). —7. *Styrax conterminus, Matuda 5507* (NY). Small divisions of scale bar = 90 μm in 2, 4–6, and 83 μm in 3, 7.

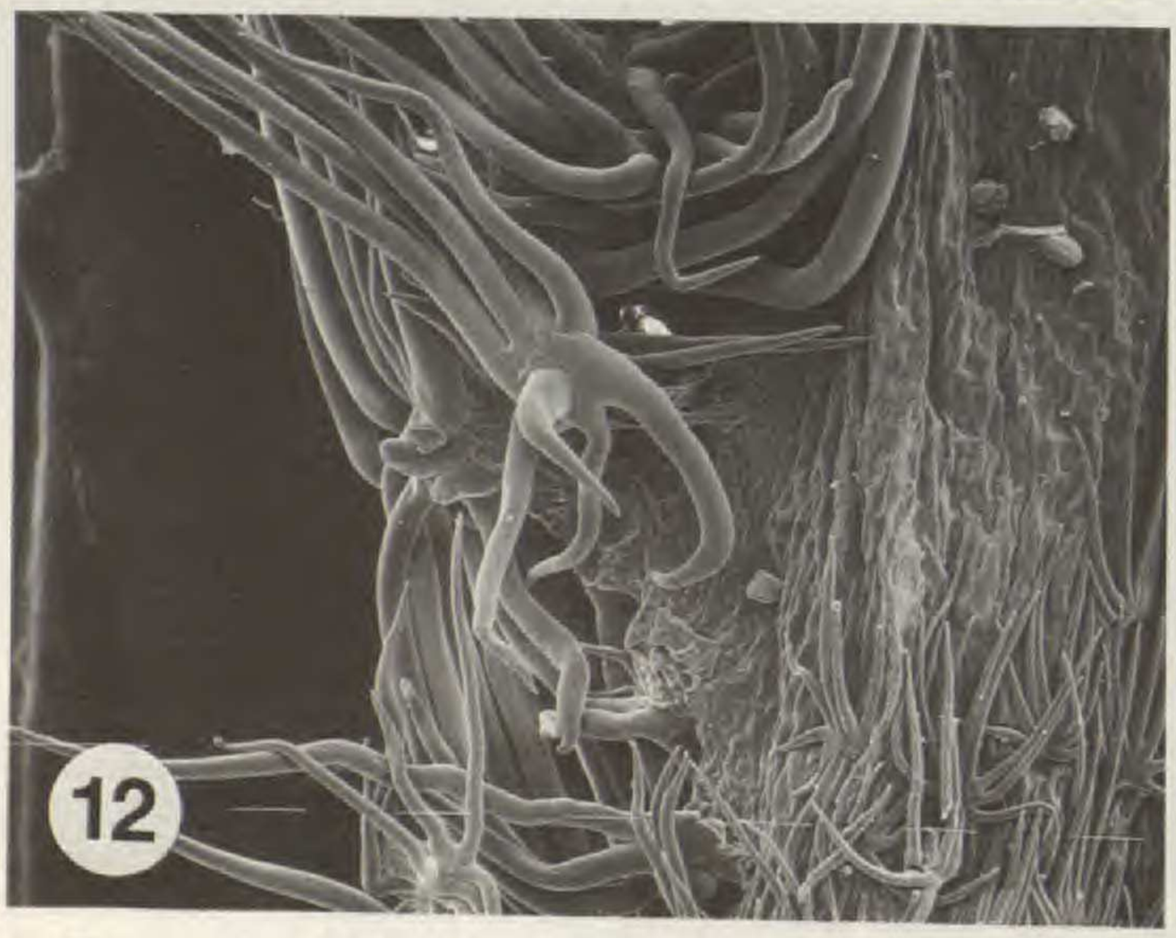
(1986) on *S. redivivus* (Torr.) L. C. Wheeler [referred to by Sugden (1986) as *S. officinale* subsp. *redivivum* (Torr.) Thorne], endemic to California. Bagging experiments showed the study population to be xenogamous. Plants were determined to be almost exclusively entomophilous, despite sucrose-dominant nectar; rarely, the flowers were visited by hummingbirds. The most common visitor was the non-native honeybee *Apis mellifera*, individuals of which were observed to forage for pollen and nectar (as did most of the bee genera that were seen to visit the species). The most efficacious pollinators

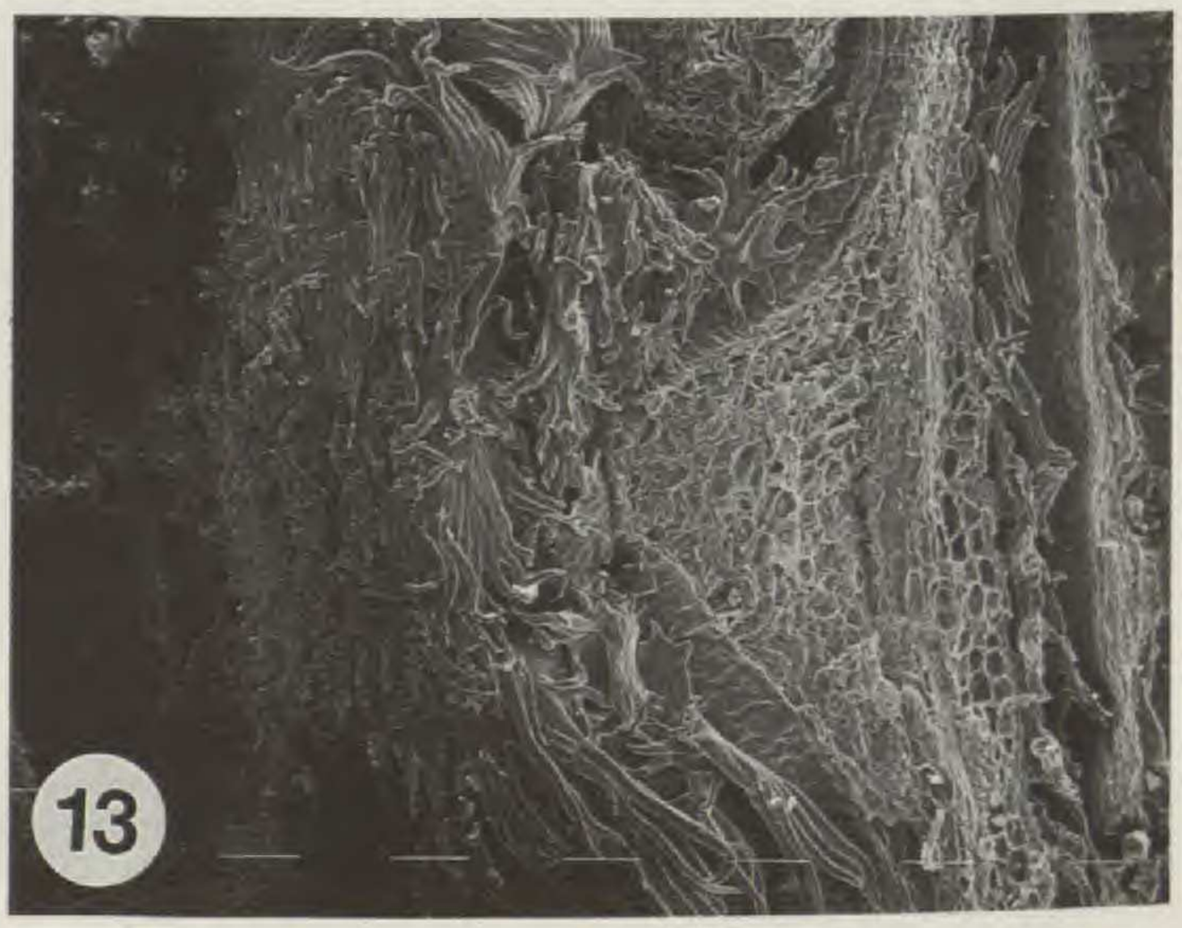












Figures 8–13. SEM micrographs of corolla vesture (8, 9) and the distinct portion of the stamen filament (10–13) in various *Styrax* taxa from Mexico and Mesoamerica. —8. Large-scaled form of *Styrax ramirezii, Conzatti 2450* (F). —9. *Styrax warscewiczii, Breedlove & Thorne 30989* (DS). —10. *Styrax warscewiczii, Breedlove & Thorne 30989* (DS). —11. *Styrax panamensis, Pittier 4242* (NY). —12. *Styrax argenteus, Breedlove 28487* (DS). —13. *Styrax peruvianus, Croat 37190* (NY). Small divisions of scale bar = 9.1 μm in 8, 8.3 μm in 9, and 90 μm in 10–13.

were butterflies of the genus *Battus*. Other common visitors were the bumble bees *Bombus edwardsii* and *B. vosnesenskii*, and the carpenter bee *Xylocopa tabaniformis*. Stellate hairs on the outer surface of the petals and on the androecium appeared to aid insect pollinators, which grasped them for support in the process of foraging. Nectar-foraging honeybees were often observed to wedge their way down against the base of the style to reach the nectaries. During this process the stigma was pushed away from the bee and did not contact it. This was considered by Sugden (1986) to be a form of nectar

"thieving," because the flower was not pollinated by the insect during this process even though it relinquished its reward.

It is not known whether the pollination syndrome documented in *S. redivivus* is typical of other *Styrax* species. Because evolution of floral morphology in *Styrax* has been conservative, the general syndrome of bee and butterfly pollination combined with xenogamy might be expected to apply across much of the genus. The flower-visiting fauna of *S. redivivus* resembles that of *S. americanus* Lam. and *S. grandifolius* Aiton, both from the southeastern United States, and sucrose-dominant nectar is also produced by *S. argenteus* (Sugden, 1986). Morphological gynodioecy has been documented for the genus *Pamphilia* (Miers, 1859) and has recently been observed (pers. obs.) in the two species of *Styrax* comprising section *Foveolaria* (*S. foveolaria* Perkins and *S. obtusifolius* Griseb.). These two *Styrax* species might be expected to exhibit a pollination syndrome divergent from that of most or all other species in the genus. Additional study of the pollination and breeding systems of a wide variety of *Styrax* species (including those of sect. *Foveolaria*) and *Pamphilia* would provide further insight into the evolution of reproductive systems in the genus.

Materials and Methods

Over 2500 herbarium specimens from 29 herbaria were examined for this study. South American material from BR, BM, CAS, F, GH, MICH, MO, NY, P, US, and W, and Asian material from GH were also examined to aid in understanding the taxonomic significance of character variation in the Mesoamerican members of the genus and to determine whether the taxa recognized here occur also in other regions. One week of fieldwork in Texas (*S. platanifolius* subspp. *stellatus* and *texanus*) and two weeks in southwestern Mexico (*S. jaliscanus* and *S. radians*) supplemented observations on the herbarium specimens.

All descriptions were derived from examination of herbarium specimens except where noted. Flowering and fruiting times, elevation ranges, habitats, distributions, common names, and uses were derived from label information of herbarium specimens. Descriptions of leaves refer to those of the fertile branches; leaves of sterile branches are consistently larger and often possess more variation in hair quantity and quality than those of fertile branches. Leaf and petiole measurements were taken from the larger examples on each herbarium sheet. All floral descriptions refer to the anthesis stage only, except where noted. Calyx dimensions are presented in terms of height (from the end of the pedicel to the apical margin) × width at the apex, and thus include the short hypanthium. Measurements of corolla length do not include the hypanthium. In the descriptions, the phrase "free portion of the stamen tube" refers to the section of the androecium from where it becomes free from the corolla to where the filaments become distinct (i.e., free from each other). Fruit length was measured from the base of the fruiting calyx to the tip of the fruit (the calyx is persistent). Fruit measurements of the drupe-bearing species were taken from the larger examples on each fruiting branch of fully expanded but unripe fruits (fully mature drupes are rarely present on herbarium specimens); those of the dry-fruited species were taken from the larger examples of mature fruits. Most observations were made by eye or with the aid of a dissecting microscope (maximum magnification = 60×). Examination of trichome morphology was supplemented with SEM.

Seven infraspecific taxa are recognized in the present treatment. The category "subspecies" has been used in all cases in accordance with the concepts of Hultén (1967) and Thorne (1978). These authors use the subspecies category for infraspecific taxa that are geographically as well as morphologically distinct.

Taxonomic Treatment

The following taxonomic treatment of *Styrax* from southern North America differs substantially from that of Gonsoulin (1974). A comparison using only Gonsoulin's annotated material shows that nearly three times as many species are recognized in the present revision as the last (Appendix 1). The number of deciduous species is lower (three vs. five) and the number of evergreen species is much higher (ten vs. two). Specimens representing six additional species were collected or accessioned subsequent to publication of the last revision (Appendix 1). The total number of species and taxa circumscribed in the present revision is 19 and 24, respectively, versus 7 and 11 in the last revision (Appendix 1). Therefore, the genus is much more diverse in Mexico and Mesoamerica than previously thought. Six new species and two new subspecies are described. In addition, three new combinations and two new species names result from this study.

Styrax L., Sp. pl. 444. 1753. TYPE: *Styrax officinalis* L. ["*officinale*"].

Strigilia Cav., Diss. 7: 358, t. 201. 1789. *Tremanthus* Pers., Syn. pl. 1: 467. 1805. TYPE: *Strigilia racemosa* Cav.

Cyrta Lour., Fl. cochinch. Ed. 1: 278. 1790. TYPE: *Cyrta agrestis* Lour.

Foveolaria Ruiz & Pav., Fl. peruv. prodr. 57, t. 9. 1794. TYPE: [not designated].
Adnaria Raf., Fl. ludov. 56. 1817. TYPE: *Adnaria odorata* Raf.
Epigenia Vell., Fl. flumin. 183. 1829. TYPE: [not designated].
Benzoin Hayne, Getreue Darstell. Gew. 11, t. 24. 1830, non Boerh. ex Schaeff., 1760. TYPE: *Benzoin officinalis* Hayne [= *Styrax benzoin* Dryand.].
Darlingtonia Torr., Proc. Amer. Assoc. Advancem. Sci. 4: 191. 1851, nom. rej. TYPE: *Darlingtonia rediviva* Torr.

Evergreen or deciduous trees or shrubs; bark smooth or cracked, gray; outer layer of older twigs fibrous, dull brown or more often gray, inner layer dull maroon; buds superposed, lepidote or stellate-pubescent, naked. Vesture consisting of scales, stalked or unstalked stellate hairs, and often sessile or stalked glandular hairs; evergreen species usually with inconspicuous scattered stalked glandular hairs on at least some of the vegetative parts: often adaxially on petiole and base of laminar midrib, abaxially on laminar surface, and on inflorescence bracteoles. Leaves alternate, simple, pinnately nerved, estipulate. Inflorescences bracteolate, axillary or false-terminal racemes or panicles, sometimes corymbose in appearance, sometimes two or more arising from the same node (or a single inflorescence branched at the base), sometimes 1–2-flowered, then usually axillary. Flowers actinomorphic, bisexual or rarely gynodioecious, fragrant, with a short hypanthium adnate to the basal third or less of the ovary wall; calyx gamosepalous beyond the hypanthium, campanulate or cupuliform, teeth (2–)4–6 or absent; corolla gamopetalous beyond the hypanthium proximally, the petals distinct distally, campanulate, the lobes 5(–10) and almost always longer than the tube, valvate or imbricate in bud, white, pink, or rarely yellow; stamens adnate to the corolla tube beyond the hypanthium proximally, free distally, 10 when the number of corolla lobes = 5, up to twice the number of the corolla lobes when the number of lobes > 5, uniseriate but appearing biseriate in bud (with five stamens in each series), the inner series often exceeding the outer at the distal end of the androecium, free portion of the filaments often connate proximally and distinct distally, sometimes completely distinct, the ventral side of the distinct portion glabrous to stellate-pubescent or lepidote and sometimes with two juxtaposed and longitudinally oriented auricles, these often obscured by a dense mass of hairs, many of which have arms predominantly oriented along the longitudinal axis of the flower, the hairs nearest the distal end of the filaments with arms predominantly pointing upward; anthers introrse, 2-locular, basifixed, longitudinally dehiscent, the anther sacs glabrous to moderately stellate-pubescent; pollen light or golden yellow; ovary superior, 3-locular at base, 1-locular toward apex; style filiform, slightly exceeding the stamens; stigma terminal, obscure, capitate or ± 3-lobed; ovules (3–5)16–24, axile or basal, anatropous. Fruit a drupe, a capsule dehiscent via 3 valves, or nut-like (dry and indehiscent), globose or ellipsoid, 1(–3)-seeded, with calyx persistent. Seed globose or ellipsoid, brown, completely filling the fruit cavity, usually smooth except for 3(–6) longitudinal grooves, with a broad hilum; endosperm copious; embryo straight; cotyledons flattened. About 120 species. U.S.A. to Argentina, E Mediterranean, E and SE Asia.

Note. The generic name *Styrax* has been treated by various authors as masculine, feminine, or neuter. Nicolson and Steyskal (1976), after conducting a thorough evaluation of the issue, advocated the use of masculine as the gender that best fits the wording of the botanical rules of nomenclature. Thus, *Styrax* is treated as masculine here.

KEY TO SPECIES OF *STYRAX* IN TEXAS, MEXICO, AND MESOAMERICA

1a. Corolla lobes imbricate in bud, partly overlapping at anthesis; fruit dry, indehiscent or dehiscent via three valves; plants deciduous (*Styrax* sect. *Styrax* ser. *Imbricatae*).
  2a. Trees to 30 m tall, small individuals not multi-stemmed from the base; lamina membranous; fruit nearly always indehiscent, rarely dehiscent via three valves, the larger fruits 10–17 mm long ... 6. *S. glabrescens*
  2b. Shrubs to 3 m tall, multi-stemmed from the base; lamina chartaceous; fruit dehiscent by three valves, the larger fruits 7–11 mm long.
    3a. Longer petioles 4–5 mm long; leaf bases subcuneate or rounded, rarely subcordate but then not attenuate; secondary and tertiary laminar veins prominent abaxially; undehisced fruit wall coarsely and weakly longitudinally striate, not transversely wrinkled post-dehiscence ..... 8. *S. jaliscanus*
    3b. Longer petioles 6–20 mm long; some leaf bases on each plant cordate or truncate and slightly attenuate; secondary and tertiary laminar veins evident but not prominent abaxially; undehisced fruit wall smooth, usually transversely wrinkled post-dehiscence ..... 14. *S. platanifolius*
1b. Corolla lobes valvate in bud, non-overlapping at anthesis; fruit a drupe; plants evergreen (*Styrax* sect. *Styrax* ser. *Valvatae*).
  4a. Abaxial laminar surface (and calyx) with vesture of peltate or lacerate-margined scales; scales at mid-calyx 0.27–0.44 mm diam.
    5a. Ventral side of the distinct portion of the stamen filaments not auriculate; leaves 2.8–3.9 times

as long as wide; connectives not or only slightly prolonged beyond the non-tapered anther sacs ..... 3. *S. conterminus*

5b. Ventral side of the distinct portion of the stamen filaments strongly auriculate; leaves 2.0–3.1 times as long as wide; connectives distinctly prolonged beyond the tapered anther sacs ..... 13. *S. peruvianus*

4b. Abaxial laminar surface with vesture of stellate hairs, or rarely radiate scales or nearly glabrous; scales at mid-calyx 0.05–0.33 mm diam., or else lacking.

6a. Leaf bases distinctly oblique ..... 18. *S. tuxtlensis*

6b. Leaf bases symmetric or only slightly oblique.

7a. Arms of the hairs nearest the distal end of the ventral side of the distinct portion of the stamen filaments predominantly pointing upward, some of these up to (0.8–)1–2 mm long; connectives distinctly prolonged beyond the tapered anther sacs.

8a. Calyx vesture uniformly golden brown; lamina 1.5 times as long as wide ..... 12. *S. panamensis*

8b. Calyx vesture predominantly or completely grayish green, occasionally with additional scattered yellow or orange-brown trichomes; lamina 2.1–3.8(–5.2) times as long as wide.

9a. Calyx vesture of stellate hairs.

10a. Larger upward-pointing hairs on the ventral side of the distinct portion of the stamen filaments with at least some arms 1–2 mm long; abaxial laminar surface and outer calyx grayish green-stellate-pubescent, without scattered orange-brown stellate hairs; larger drupes 13–18 mm long (excluding beak, if present), ellipsoid or ovoid-ellipsoid; corolla lobes 1.7–2.3 mm wide, widely spreading or recurved ..... 1. *S. argenteus*

10b. Larger upward-pointing hairs on the ventral side of the distinct portion of the stamen filaments with arms to 1 mm long; abaxial laminar surface and outer calyx with scattered, orange-brown, stellate hairs in addition to grayish green pubescence; larger drupes (15–)17–28 mm long, ovoid or obovoid; corolla lobes 2.5–4 mm wide, recurved or reflexed ..... 11. *S. nicaraguensis*

9b. Calyx vesture of radiate scales.

11a. Abaxial laminar surface glabrous or nearly so; calyx 4–7 mm long, in fruit funnelform, 4–8 mm long; anthers 5–8 mm long; corolla lobes linear-deltoid ..... 5. *S. glabratus*

11b. Abaxial laminar surface densely pubescent; calyx 2.5–3 mm long, in fruit shallowly cupuliform, to 1.5 mm long; anthers 4.5 mm long; corolla lobes linear ..... 17. *S. steyermarkii*

7b. Arms of the hairs nearest the distal end of the ventral side of the distinct portion of the stamen filaments not predominantly pointing upward, typically not exceeding 0.5(–0.7) mm long; connectives not or only slightly prolonged beyond the non-tapered anther sacs.

12a. Calyx teeth 1–2 mm long, contiguous ..... 4. *S. gentryi*

12b. Calyx teeth 0–0.6 mm long, not contiguous.

13a. Vesture just below mid-calyx of radiate scales.

14a. Vesture on the outer distal third of the corolla lobes of stellate hairs; anthers 3.0–4.8 mm long, 1.9–5.3 times as long as the distinct portion of the filaments ..... 16. *S. ramirezii*

14b. Vesture on the outer distal third of the corolla lobes of radiate scales; anthers 1.7–3.6 mm long, 1.1–2.2 times as long as the distinct portion of the filaments ..... 19. *S. warscewiczii*

13b. Vesture just below mid-calyx predominantly of stellate hairs, sometimes also with a few scale-like hairs scattered among the stellate ones.

15a. Abaxial surface of the secondary and tertiary veins obscured by the tomentum; ± evenly scattered, orange-brown hairs (in addition to whitish pubescence) present on the abaxial surface of most or all fully expanded leaves.

16a. Laminae chartaceous, lanceolate, the larger 7.7–9.7 cm long; fruit 9–11 mm long; corolla 11–15(–17) mm long, white ..... 9. *S. lanceolatus*

16b. Laminae thick-chartaceous, elliptic, slightly oblanceolate, or ovate, the larger 11–18 cm long; fruit 17–19 mm long (unknown in *S. incarnatus*); corolla (10–)14–24 mm long, usually pink, sometimes white.

17a. Larger laminae 3.5–5 cm wide, usually narrowly elliptic, sometimes slightly oblanceolate, slightly ovate, or elliptic; lower pedicels 11–15 mm long; calyx 4–5 × 5–6 mm ..... 2. *S. austromexicanus*

17b. Larger laminae 5.5–9.5 cm wide, ovate or broadly elliptic; lower pedicels 3–9 mm long; calyx 3–3.5 × 2.5–4.5 mm ..... 7. *S. incarnatus*

15b. Abaxial surface of the secondary and tertiary veins evident; orange-brown hairs on the abaxial surface of fully expanded leaves at most sporadically present on some of the veins, otherwise nearly always absent.
18a. Larger fruits 15–20 × 9–12 mm; lamina usually obovate, sometimes broadly elliptic ..... 10. *S. magnus*
18b. Larger fruits 7–15 × 5–9 mm; lamina ovate-oblong or elliptic, sometimes lanceolate, suborbicular, or ovate.
19a. Distinct portion of stamen filaments 2.5–3.5 mm long; abaxial laminar surface usually soft to the touch; calyx not stellate-villous; corolla white, thin, the petals connate up to the calyx margin, the lobes moderately or widely spreading; stigma 0.6–0.8 mm wide ..... 15. *S. radians*
19b. Distinct portion of stamen filaments 0.6–2.0(–2.6) mm long; abaxial laminar surface slightly or moderately rough or rarely soft to the touch, if soft then at least the lower third of the calyx villous; corolla white or pink, thickened, the petals connate 1–3 mm beyond the calyx margin distally, the lobes slightly spreading; stigma 0.3–0.5 mm wide ..... 16. *S. ramirezii*

1. Styrax argenteus C. Presl, Reliq. haenk. 2: 60. 1831–1835. *Strigilia argentea* (C. Presl) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 282. 1859. TYPE: Mexico. Guerrero: "Ad portum et urbem Acapulco" (protologue), *T. Haenke s.n.* (or *148*; Perkins, 1907) (holotype, PR not seen; isotypes, F, MO, W, photo of W in A, F, MICH). Figures 2, 12, 14–16.

Styrax myristicifolius Perkins, Bot. Jahrb. Syst. 31: 481. 1902. TYPE: Guatemala. Santa Rosa: Las Viñas, Sep. 1894, *Heyde & Lux 6182* (lectotype, designated by Standley & Williams (1967), F; isolectotypes, GH, MO, NY, US).

Styrax polyanthus Perkins, Bot. Jahrb. Syst. 31: 479. 1902. TYPE: Guatemala. Guatemala: prope Guatemala, February 1890, *J. Donnell Smith 2266* (lectotype, designated by D'Arcy (1979), US; isolectotypes, F, GH).

Evergreen tree to 20(–30) m. Young twigs grayish yellow-, yellowish brown-, light brown-, or orange-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 10–25 mm long. Lamina chartaceous, 6.5–18 × 2.4–7.5 cm, 2.1–3.7 times as long as wide, ovate, lanceolate, narrowly or broadly elliptic, or rarely slightly oblanceolate, secondary veins 9–11; apex acute to acuminate; base cuneate to rounded, often slightly attenuate, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute grayish green stellate hairs and often also larger, soft, grayish green or yellowish brown stellate hairs, the minute hairs usually absent from the primary through tertiary veins, thus the vein surface easily visible; margin entire. Inflorescences axillary or false-terminal, racemose or rarely paniculate, the racemes or panicle branches 3–14 cm long, 3–22-flowered. Lower pedicels 2–11(–15) mm long. Calyx 2.5–5.0 × (3.5–)4–6(–7) mm, cupuliform or broadly cupuliform, grayish green-stellate-pubescent; calyx teeth 5, to 0.5 mm long, deltoid, calyx margin truncate or rarely slightly concave between the teeth, inner margin often glandular. Corolla white, 10–16 mm long, petals usually connate up to the calyx margin, rarely to 2 mm distally beyond; corolla lobes 5, valvate in bud, 8–14 × 1.7–2.3 mm, non-overlapping, widely spreading or recurved, thin, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0.7–1 mm long; distinct portion of filament 2–2.5 mm long, of equal width throughout, ventrally with small auricles bearing a dense mass of white stellate, stiff hairs with at least some arms 1–2 mm long, the hairs nearest the distal end of the filament with arms predominantly pointing upward, also pubescent below the auricles and at the sinus between adjacent filaments; anthers (5–)6–8 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely stellate-hirsute; style glabrous, or pubescent at base only; stigma 0.3–0.5 mm wide. Drupe 13–18 × 8–14 mm (wider when 2-seeded; does not include occasional beak), ellipsoid or ovoid-ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Near Acapulco, Guerrero, Mexico, to central Panama; most common on the Pacific slope of the cordillera of Central America; one collection from Cayo District, Belize; 100–1700 m; tropical humid forests, seasonal evergreen forests with *Pinus* and *Quercus,* tropical deciduous forests, pastures, open scrub, coffee plantations; found often along waterways with other riparian vegetation, and in moist ravines, but also on dry limestone ridges, at forest edges, disturbed slopes, and with various types of

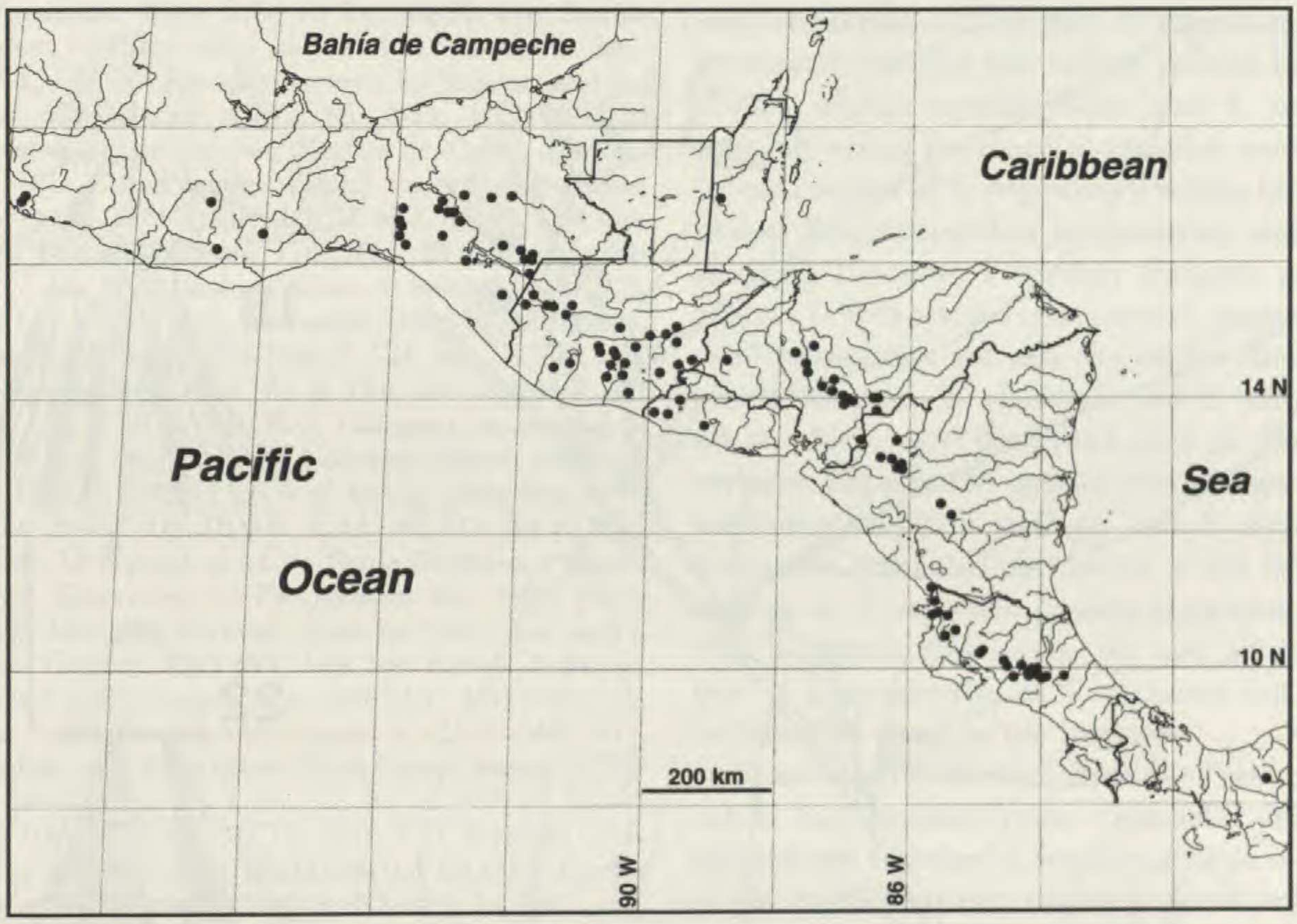


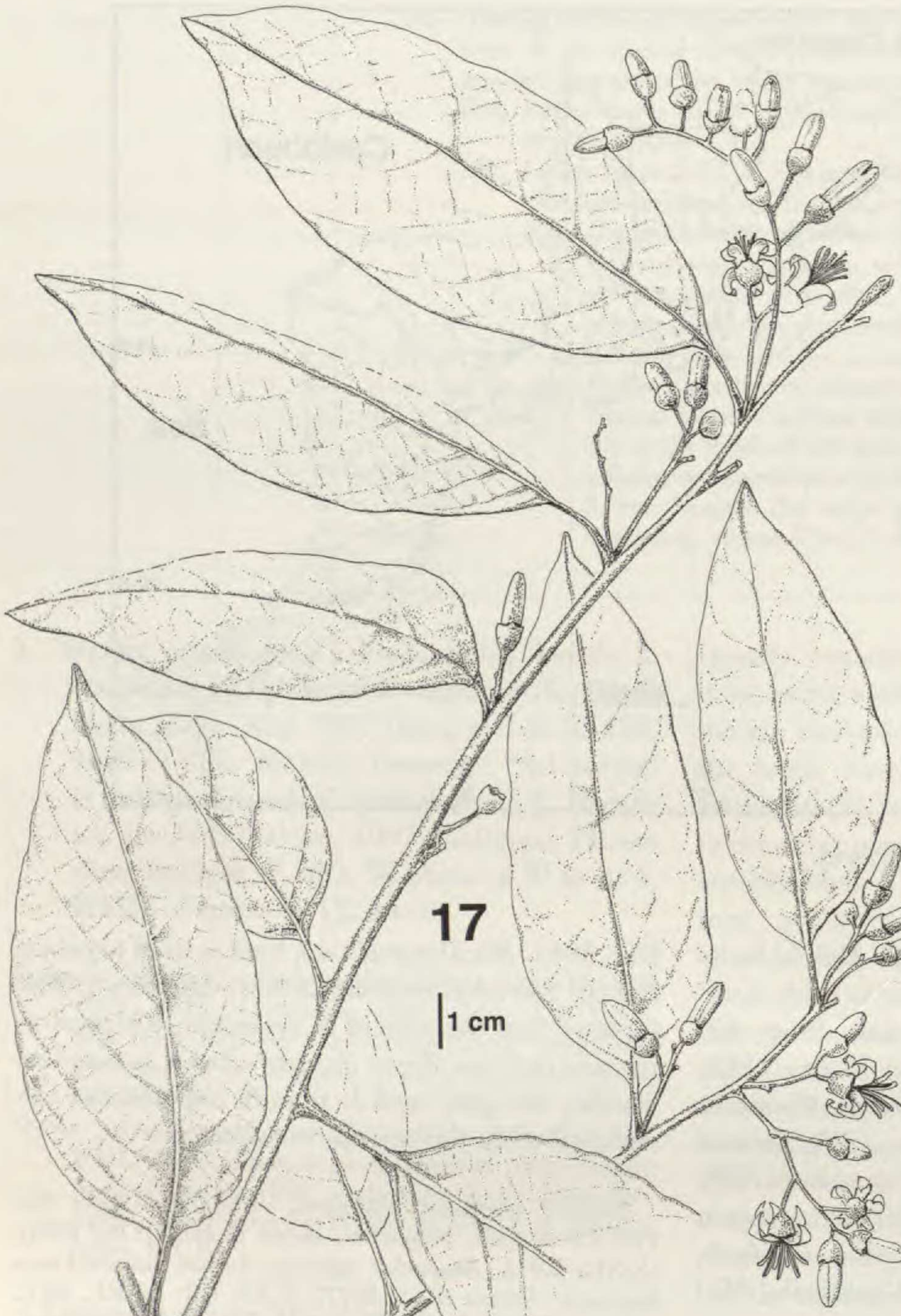
Figure 14. Distribution of *Styrax argenteus*.

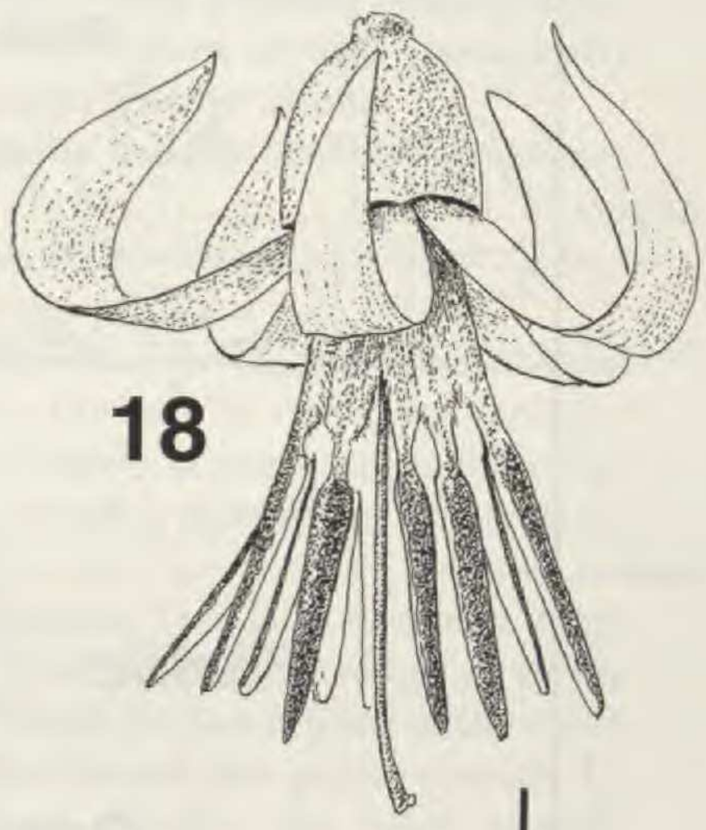
secondary growth. Flowering: August–March; fruiting: October–May.

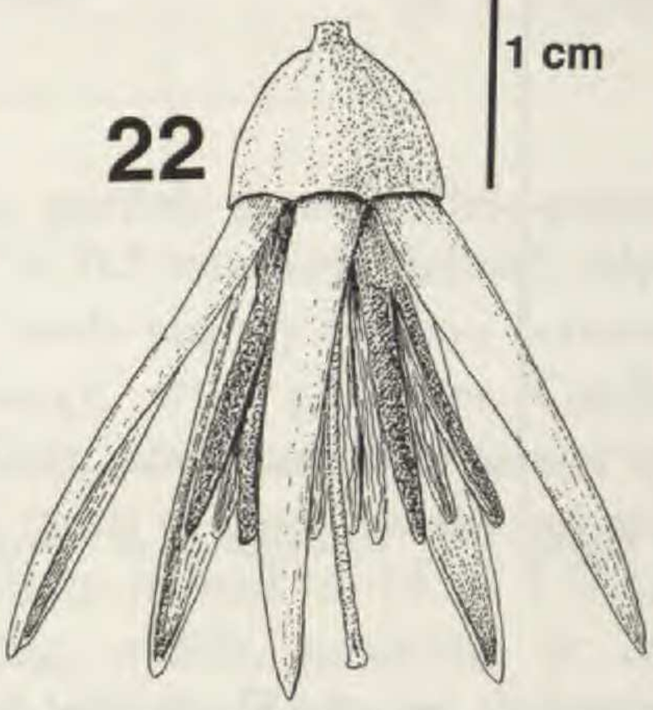
Common names. Alamo (Honduras, *Erazo 63, Standley 15947, von Hagen & von Hagen 1253*; Nicaragua, "*T-1*" *s.n.*), alomo (Honduras, *Molina & Molina 34417*), chucam-ai (Chiapas, 1919, *Becerra s.n.*), duraznillo (Guatemala, *Steyermark 51100*), estorac (El Salvador, *Standley 20147*), estoraco (Costa Rica), estoraque (El Salvador, *Calderón 1404* and *1405, Standley 20405*; Guatemala, *Morales 1208, Steyermark 50801*), estoraque común (Guatemala, *Aguilar 186* and *214*), naranjo (Guatemala, *Standley 82830*), palo blanco (Honduras, *Erazo 63, Molina 20321*), roble (Guatemala, *Steyermark 30624*), tepe aguacate (Guatemala, *Steyermark 50699*). Standley (1924) has listed additional common names for this species: bracino (Costa Rica), capulín (Oaxaca), chilacuate (Guerrero, Michoacán), estorac (El Salvador), hoja de jabón (Oaxaca), resina, resino (Costa Rica, Nicaragua), ruín (Sinaloa), and sahumerio (Panama), but because his circumscription of *S. argenteus* differs from mine, the application of these names in this revision is ambiguous. In Standley (1938) the names listed (bracino, laurel, resina, tubús; Costa Rica) are more likely to apply to *S. argenteus* as conceptualized in Standley (1924).

Uses. Fruits are sold in local markets (Chiapas, *Bauml et al. 531*); flowers are boiled with lime leaves and the water used as a perfume (Oaxaca, Dec. 1961, *MacDougall s.n.*); bark is used to poison fish (El Salvador, *Standley 20405*). Standley (1924) reported that the gum of *S. argenteus* is burned as incense in Costa Rican churches, but it is not clear whether the gum used is from *S. argenteus* as circumscribed in the present revision.

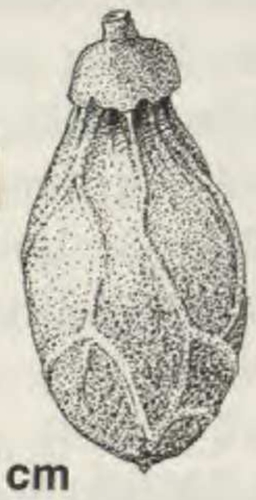
Selected specimens examined. BELIZE. **Cayo:** Río Frío Caves road, Augustine, *Meave & Howe 1162* (MO). COSTA RICA. **Alajuela:** Santiago de San Ramón-Finca Barranca, *Gómez et al. 20777* (CAS, CR, DUKE, MO). **Cartago:** Turrialba, *Córdoba 754* (CR, DUKE). **Guanacaste:** Parque Rincón de la Vieja, Hacienda Santa María, *Herrera 854* (CR, F, MO, TEX). **Heredia:** Heredia, *Williams 16067* (F, GH). **Puntarenas:** Monteverde, San Luis Valley, *Haber ex Bello 3533* (CR, DUKE, F, MO, TEX, W). **San José:** 1.4 km NW of Brazil de Santa Ana, *Taylor 17390* (F, MO, US). EL SALVADOR. **Ahuachapán:** Sierra de Apaneca, *Standley 20147* (GH, NY, US). **San Salvador:** Comasagua, *Calderón 1404* (GH, NY, US). **Santa Ana:** vicinity of Santa Ana, *Standley 20405* (GH, NY, US). GUATEMALA. **Baja Verapaz:** 10 mi. S of Rabinal, *Harmon & Dwyer 3056* (GH, MO, NY). **Chimaltenango:** along road from Chimaltenango to San Martín Jilotepeque, *Standley 57958* (F, NY). **Chiquimula:** along Tepotun River, vicinity of Esquipulas, *Molina & Molina 25328* (F, MO, US). **El Progreso:** Sierra de las Minas, 1 Jan. 1908, *Kellerman s.n.* (F). **Escuintla:** below Las Lajas, *Standley 64767* (A, F). **Guatemala:** Guatemala City, *Harmon 3461* (DS, MICH, MO, NY). **Huehuetenango:** Aguacatán, *Skutch 1935* (A, F, NY); Puente El Aguilar, just E of San Sebastián, *Standley 82830* (F, MO, US). **Jutiapa:** Quebrada above Ovejero, *Standley 77656* (F). **Quiché:** *Aguilar 758* (F). **Santa Rosa:** Volcán Tecuamburro, N of Chiquimulilla, *Steyermark 33138* (A, F). **Sololá:** Finca Belén,





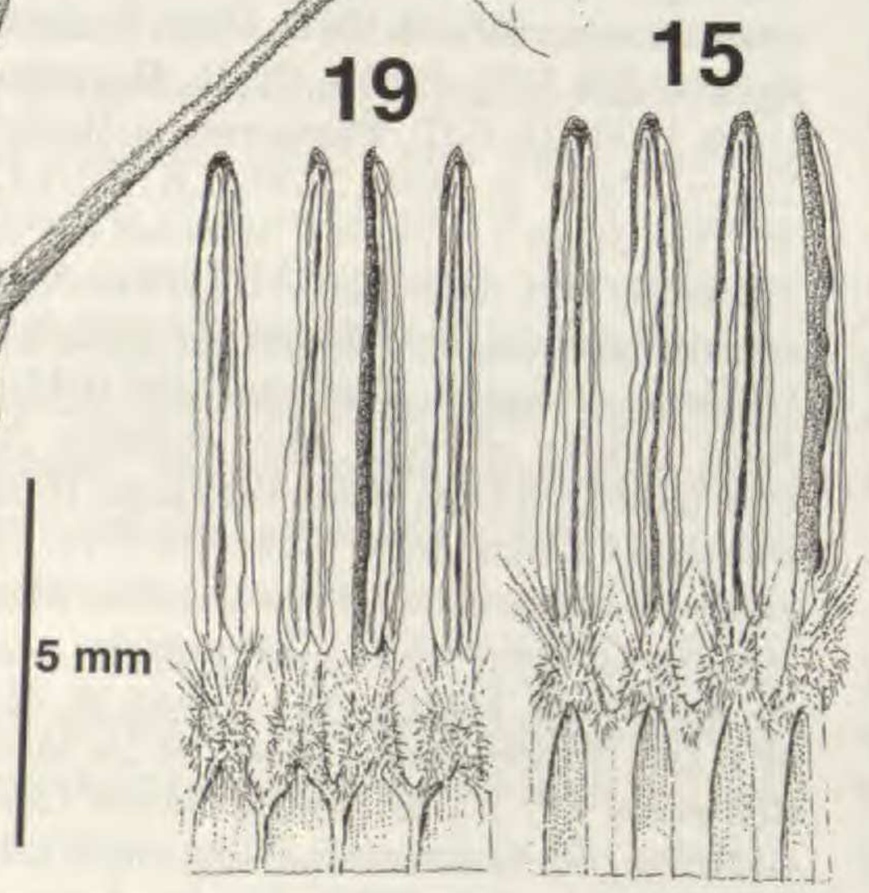














Figures 15–24. 15, 16. *Styrax argenteus.* —15. Four adjacent stamens, *Palacios 34* (CAS). —16. Fruit, *Skutch 1935* (F). 17–20. *Styrax nicaraguensis* subsp. *nicaraguensis.* —17. Flowering branch. —18. Flower. —19. Four adjacent stamens. 17–19, *Webster et al. 12496* (LL). —20. Fruit, *Atwood s.n.* 8 June 1975 (MO). —21. *Styrax nicaraguensis* subsp. *ellipsoidalis,* fruit; *Dryer 1420* (F). 22–24. *Styrax steyermarkii.* —22. Flower. —23. Four adjacent stamens, *Lundell & Contreras 19214* (LL). —24. Fruit. 22, 24. *Lundell & Contreras 21219* (LL).

Lake Amatitlán, *White 5260* (F, LL, MICH, US). **Suchitepéquez:** southern lower slopes of Volcán Zunil, *Steyermark 35418* (F). **Zacapa:** between La Reforma and Teculután, *Steyermark 42075* (F, NY). HONDURAS. **Choluteca:** vicinity of San Marcos de Colón, *Standley 15875* (F). **Comayagua:** plains near Siguatepeque, *Yuncker et al. 5589* (F, GH, MICH, MO, NY, U, US). **Copán:** El Polvazal, *Ferrera 176* (NY). **El Paraíso:** near Arenar, 5 km W of Danli, *Williams & Molina 10491* (DS, F, GH, LL, MICH, MO). **Morazán:** near Cuesta Grande, *Williams & Molina 13270* (BH, F, GH, LL, MEXU, MO, US). **Tegucigalpa:** Mont. de la Flor, *von Hagen & von Hagen 1253* (F, NY). MEXICO. **Chiapas:** Intersection of Hwy. 190 and road to Tuxtla Gutiérrez airport, *Bauml et al. 531* (MICH, US); 13 km N of Arriaga along Hwy. 195, *Breedlove 28487* (DS, DUKE, F, LL, MEXU, MICH, MO, NY, RSA); El Zapotal, al SE de Tuxtla Gutiérrez, *Palacios 34* (CAS). **Guerrero:** La Providencia, Mar. 1926, *Ferris s.n.* (DS). **Oaxaca:** between Trapiche Santa Ana and T. del Lazo, *Conzatti 4558* (NY, US); San Bartolo Yautepec, Dec. 1961, *MagDougall s.n.* (MEXU). NICARAGUA. **Boaco:** Cerro Mombachito, *Aranda et al. 40* (MO, NY). **Chontales:** ca. 2.8 km above (N of) Cuapa, *Stevens 22709* (MO). **Estelí:** Paso de León, 3.5 km al NW de Estelí, *Moreno 10854* (DUKE, MEXU, MO, NY). **Madriz:** Cerro El Fraile, *Moreno 23512* (MEXU, MO). PANAMA. **Coclé:** vicinity of Olá, *Pittier 5076* (GH, NY, US).

Styrax argenteus is one of the most common species of *Styrax* in the area circumscribed by this revision. It is distinguished from sympatric species by its evergreen leaves, grayish green stellate pubescence on the lower laminar surface and calyx (i.e., no orange-brown hairs), corolla lobes united up to the calyx margin, and slightly auriculate stamen filaments bearing long-armed and relatively stiff stellate hairs ventrally; the hairs nearest the distal end of the filament possess the longest arms, which predominantly point upward. It is a relatively low-elevation species, unlike most other *Styrax* species in the region. Generally this species does not extend lower than 400 m, but it does occur at or below 100 m in Guanacaste Province, Costa Rica (OTS Research Area A, *Frankie 239a*) and Coclé Province, Panama (*Pittier 5076*).

The differences between *S. argenteus* and *S. nicaraguensis* are subtle. *Styrax nicaraguensis* has orange-brown hairs on the calyx and the lower laminar surface, a larger drupe, a highly restricted range, and a different habitat. Sterile specimens of *S. argenteus* are difficult to distinguish from the equally common *S. warscewiczii*: *S. argenteus* tends to have larger leaves that are fulvescent when young, and often has longer, relatively loose and soft hairs abaxially. However, some sterile specimens cannot be determined, particularly those from saplings or stump sprouts, or from undocumented elevations and/or habitats.

My treatment of *S. argenteus* differs from those of Perkins (1907) and Gonsoulin (1974). I agree with Gonsoulin (1974) that *S. argenteus* was unnecessarily divided into several species by Perkins (1902). *Styrax myristicifolius* and *S. polyanthus* both fall within the range of variation encompassed by my concept of *S. argenteus* [Perkins later (1907) placed *S. myristicifolius* in synonymy under *S. argenteus*]. However, I strongly disagree with Gonsoulin's (1974) revised concept of *S. argenteus*. This concept includes not only the clearly distinct species *S. magnus*, *S. ramirezii*, and *S. warscewiczii*, all of which were described prior to Gonsoulin's revision, but also the species now recognized as *S. austromexicanus*, *S. radians*, and *S. steyermarkii*. Gonsoulin annotated specimens of the latter three species as *S. argenteus* despite examining material with diagnostic characters. He also annotated the type of *S. panamensis* as *S. argenteus* but failed to include this name in the treatment.

To account for the high amount of variation present in his circumscription, Gonsoulin (1974) recognized two varieties of *Styrax argenteus* in addition to the typical variety: variety *hintonii* and variety *ramirezii* (= var. *micranthus*). The three varieties were distinguished by the type and amount of pubescence on the lower laminar surface and the calyx, but essentially exhibited no ecological or geographic distinctions. Although calyx hair types are critical characters in the delimitation of *Styrax* species, the hairs on the lower laminar surface tend to be more variable and unreliable. When Gonsoulin attempted to reconcile the relatively constant nature of the calyx pubescence with the variable nature of the leaf pubescence, the result was the recognition of a large number of intermediates throughout the ranges of the varieties. For example, *S. argenteus* var. *ramirezii* is distinguished from variety *argenteus* by a thin versus thick tomentum on the lower laminar surface. However, *S. argenteus* in my view is polymorphic for this character in that individuals always possess the thin tomentum, but in addition often have an additional layer of longer hairs. The majority of specimens examined by Gonsoulin that are assigned here to *S. argenteus* were annotated by him as variety *argenteus*, primarily because *S. argenteus* usually possesses the longer hairs. However, a considerable portion were annotated as variety *ramirezii* (those with the long pubescence absent), or intermediates between this and the typical variety. When the hairs are unusually long, specimens of *S. argenteus* were annotated by Gonsoulin as variety *hintonii* or as a variety *hintonii* intermediate (it is never stated what the second taxon is in cases of purported intermediacy). The high number of intermediates assigned to variety *argenteus* and variety *ramirezii* by Gonsoulin

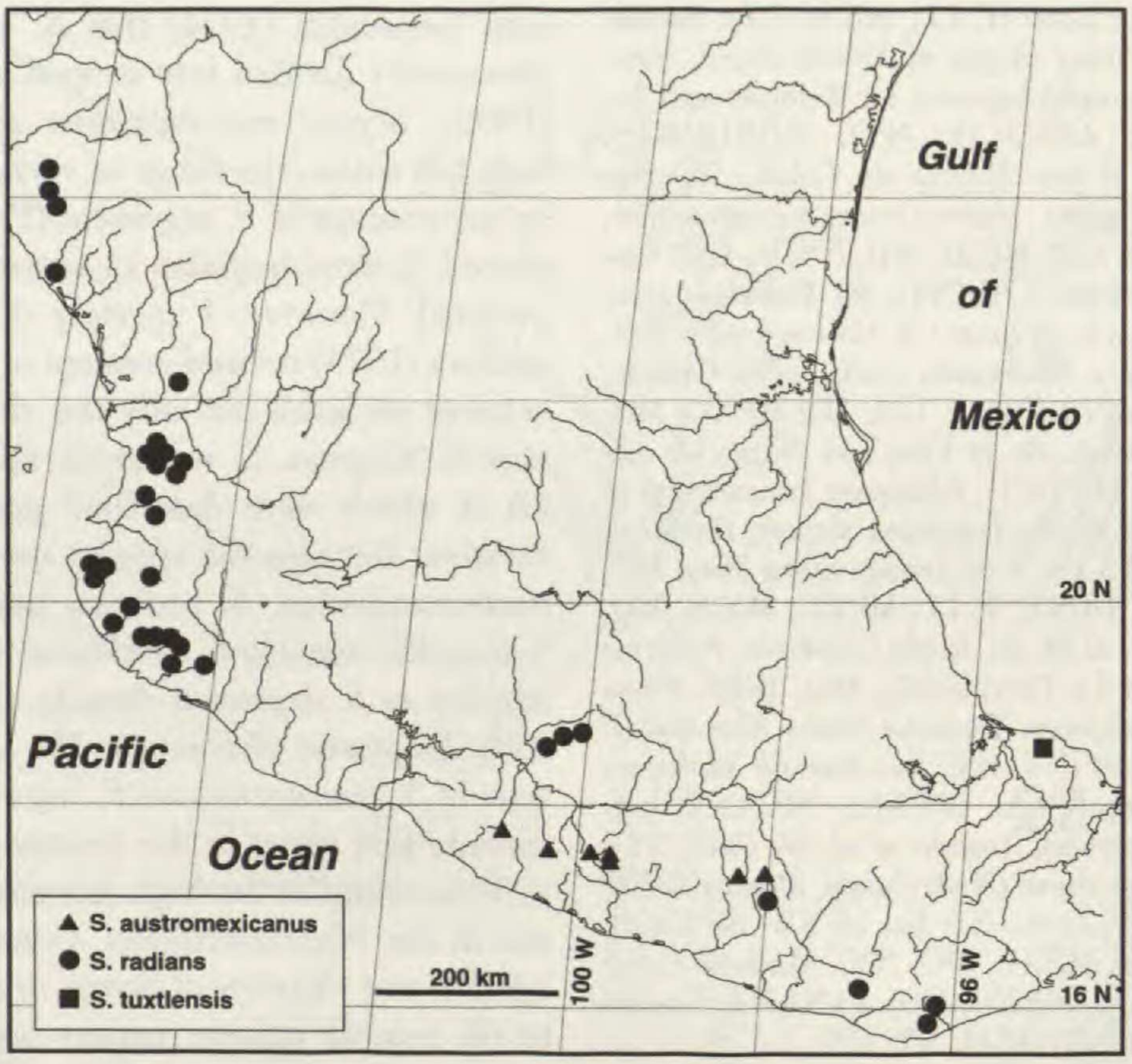


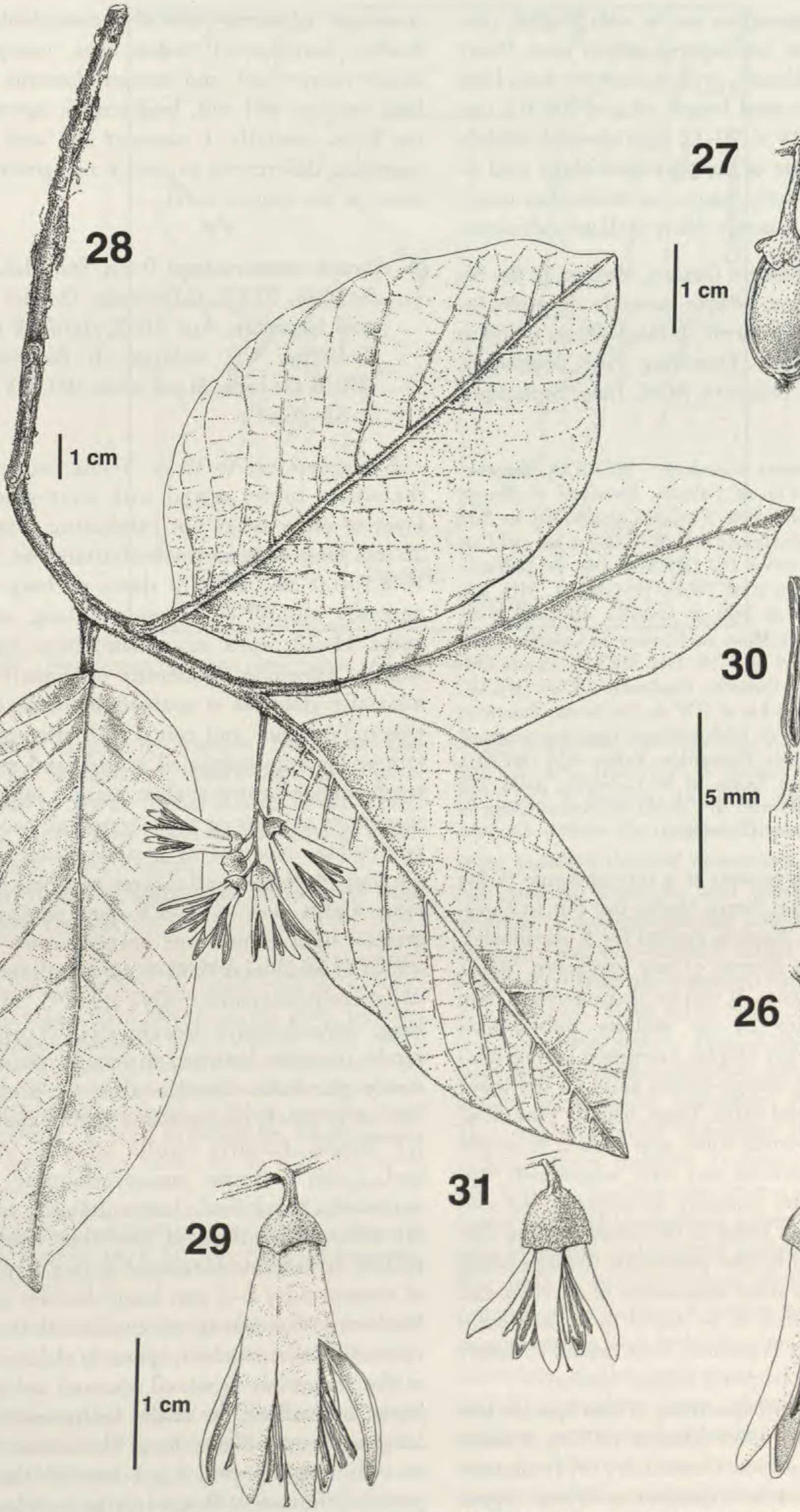
Figure 25. Distribution of *Styrax austromexicanus*, *S. radians* and *S. tuxtlensis*.

is accounted for to a large extent by the variable amount of the longer hairs present in individuals of *S. argenteus*. In the present treatment *S. argenteus* vars. *ramirezii* and *hintonii* are synonyms of *S. ramirezii*.

The collection date of the type of *S. argenteus* is probably October–December 1791 (McKelvey, 1955).

2. Styrax austromexicanus P. W. Fritsch, nom. et stat. nov. Based on: *Styrax argenteus* var. *grandiflorus* E. Carranza, Acta Bot. Mex. 36: 15. 1996, non *S. grandiflorus* Griff., 1854. TYPE: Mexico. Oaxaca: Mpio. de Juxtlahuaca, 3 km S of the road to San Martín Peras on the road to Coicoyán de Las Flores, 27 Sep. 1993, *J. L. Panero et al. 3475* (holotype, MEXU not seen; isotypes, ENCB not seen, IEB not seen, MSC). Figures 25–27.

Evergreen tree to 17 m. Young twigs predominantly and densely orange-brown-stellate-pubescent or -villous, with intermixed scattered short-armed white stellate hairs; outer layer of older twigs not exfoliating. Petiole 13–21 mm long. Lamina thick-chartaceous, 11–18 × 3.5–5 cm, usually narrowly elliptic, sometimes slightly oblanceolate, slightly ovate, or elliptic, secondary veins about 13; apex acute to abruptly acuminate; base cuneate to subrounded, symmetric or slightly oblique; adaxially glabrous except along the major veins or rarely sparsely stellate-pubescent; abaxially covered with minute whitish stellate hairs, larger whitish hairs and evenly scattered orange-brown hairs, the three types occurring on the secondary and tertiary veins, thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, racemes or panicle branches 3.5–6.5 cm long, 2–11-flowered. Lower pedicels 11–15 mm long. Calyx 4–5 × 5–6 mm, conical or broadly cupuliform, light grayish green-stellate-pubescent, with a variable amount of larger orange-brown stellate hairs; calyx teeth 5, to 0.5 mm long, deltoid or more often indistinct from the calyx margin, rarely absent, calyx margin truncate or more often slightly concave between the teeth, inner margin rarely glandular. Corolla pink or white, 14–23 mm long, petals connate 2–5 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 8–17 × 2.5–3.5 mm, non-overlapping, erect or spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 3.5–6 mm long; distinct portion of filament 1.5–2 mm long, of equal width throughout, ventrally not auriculate, sparsely white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.5 mm long; anthers 4.5–5.2



Figures 26–31. 26, 27. *Styrax austromexicanus.* —26. Pedicel and flower, *Hinton et al. 14750* (F) —27. Fruit, *Rzedowski 18529* (TEX). 28–30. *Styrax incarnatus, Lundell & Contreras 19618* (LL). —28. Flowering branch. —29. Pedicel and flower. —30. Four adjacent stamens. —31. *Styrax lanceolatus*, pedicel and flower; *Johnston 7408* (TEX).

mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style pubescent from base to 45–90% of the total length; stigma 0.3–0.5 mm wide. Drupe 17–19 × 10–12 mm, obovoid, slightly beaked by the base of the persistent style; wall irregularly and coarsely rugose on herbarium specimens. Seed coat sparsely white-stellate-pubescent.

Guerrero and western Oaxaca, Mexico, in the Sierra Madre del Sur; bosque mesofilo de montaña, *Quercus-Pinus-Abies* forest; 2100–3000 m; found in rocky limestone areas. Flowering: June, September, October; fruiting: February, April, June, September, November.

Additional specimens examined. MEXICO. **Guerrero:** 16 km SW of Filo de Caballo, *Breedlove & Almeda 64929* (CAS); W of Puerto El Gallo along road to Toro Muerto, *Breedlove & Almeda 65176* (CAS); 4 km del Carrizal de Bravos, *Fonseca 163* (MEXU); Dto. de Galeana, Piedra Ancha, *Hinton et al. 14750* (F, GH, LL, MO, NY, US); 11 km al SW de Filo de Caballo, *Martínez et al. 4906* (F, LL, MEXU); Mpio. de Coyuca de Catalán, Cerro del Chivo, *Medrano et al. 6706* (GH, MEXU); Puerto Chico, 10 km al W de Camotla, *Rzedowski 18529* (MEXU, MICH, RSA, TEX); 6 km al NW de Omiltemi, *Tenorio et al. 2642* (MO); Mpio. de Chilpancingo, entre los cerros de la Aguililla y Plan de Potrerillos, *Valdez 616* (MEXU). **Oaxaca:** E de Xatu Yahta, al W Coicoyán, *Avila 742* (CAS); km 18 on the road to Cañada de Lobos, Gorge of the Río Ratón, *Panero 5254* (MSC).

Styrax austromexicanus is a rare endemic to the cloud forests of the Sierra Madre del Sur in Guerrero and Oaxaca, Mexico. Except for *S. incarnatus,* it has the largest flowers of any evergreen *Styrax* species in the region. It can be distinguished from sympatric species by its stellate pubescence throughout, narrowly elliptic evergreen leaves, mixture of white and orange-brown hairs on the lower laminar surface and calyx, large, usually pink flowers with a long corolla tube, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. In addition, the secondary and tertiary veins of the lower laminar surface are obscured by the tomentum, distinguishing this species from most specimens of *S. ramirezii.* This species appears to be allied to *S. incarnatus* of Guatemala and Honduras, from which it differs principally by its narrowly elliptic leaves.

As the first known specimen of this species was not collected until 1939 (*Hinton 14750*), Perkins did not see this species. Gonsoulin (1974) annotated both collections he examined as *Styrax argenteus* var. *argenteus,* and Carranza (1996) also considered this species to be a variety of *S. argenteus* (var. *grandiflorus*). However, in contrast to *S. argenteus* as circumscribed here, *S. austromexicanus* possesses white or pink (vs. consistently white) flowers, non-tapered anther sacs, non-prolonged anther connectives, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. I consider the sum of these character differences to justify recognition of this taxon at the species level.

3. Styrax conterminus Donn. Sm., Bot. Gaz. 18: 5. 1893. TYPE: Guatemala. Quiché: San Miguel Uspantán, Apr. 1892, *Heyde & Lux 2915* (holotype, US; isotypes, B destroyed, GH, HRCB not seen, M not seen, MO, NY). Figures 7, 32–35.

Evergreen tree to 18 m. Young twigs lepidote, the scales brown mixed with olive-green; outer layer of older twigs not exfoliating. Petiole 13–25 mm long. Lamina thick-chartaceous, 8.5–16.5 × 2.7–5.0 cm, 2.8–3.9 times as long as wide, narrowly elliptic or narrowly oblong, secondary veins 11–13; apex acuminate; base cuneate to slightly attenuate, symmetric or slightly oblique; adaxially glabrous or sparsely lepidote; abaxially covered (surface and veins) with olive-green peltate or lacerate-margined scales, and more scattered orange-brown scales; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, racemes or panicle branches 3–5.5 cm long, 4–9-flowered. Lower pedicels 8–12 mm long. Calyx 3–4 × 4–5.5 mm, conical, olive-green-, light brown-, or orange-brown-lepidote, scales at mid-calyx 0.33–0.42 mm diam., peltate or lacerate-margined; calyx teeth 5, to 0.7 mm long, deltoid; calyx margin slightly concave or rarely truncate between the teeth, inner margin rarely glandular. Corolla white or pink, 10–13 mm long, petals connate 2–4 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 7–10 × 3 mm, non-overlapping, erect or spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of peltate or lacerate-margined scales. Free portion of stamen tube 2–3 mm long; distinct portion of filament 1–2 mm long, of equal width throughout, ventrally not auriculate, sparsely radiate-lepidote at the somewhat incurved filament margins, glabrous on the face, the scales with arms to 0.4 mm long; anthers 3.5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary lepidote; style glabrous or pubescent at base only; stigma 0.4–0.5(–0.8) mm wide. Drupe 12–15 × 7–9 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

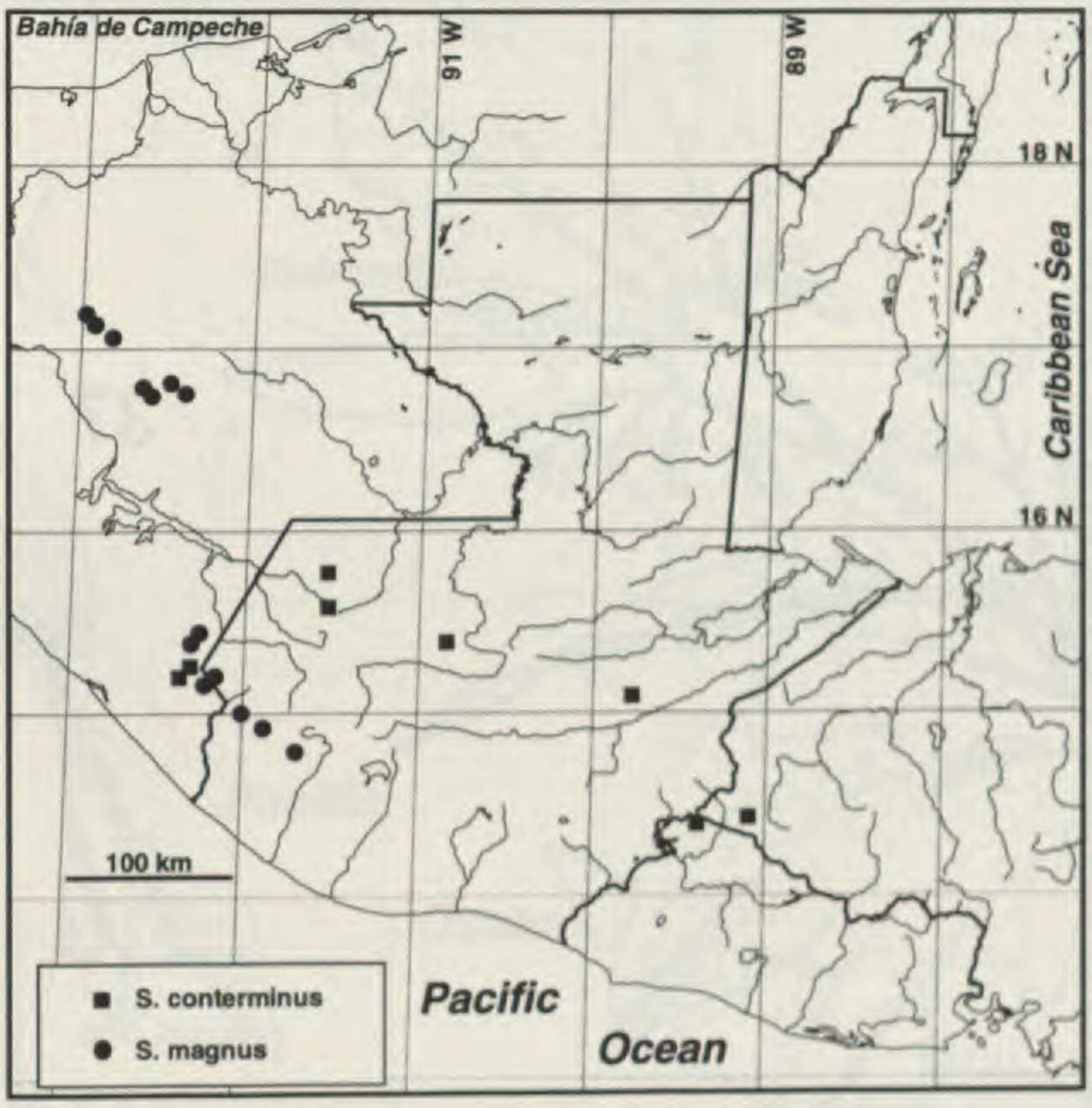


Figure 32. Distribution of *Styrax conterminus* and *S. magnus.*

Southern Chiapas to western Honduras and northern El Salvador; ± 1500–2800 m; *Pinus-Quercus-Ostrya* forest, broad-leaved cloud forest. Flowering: April–June, December; fruiting: January, February, June, August.

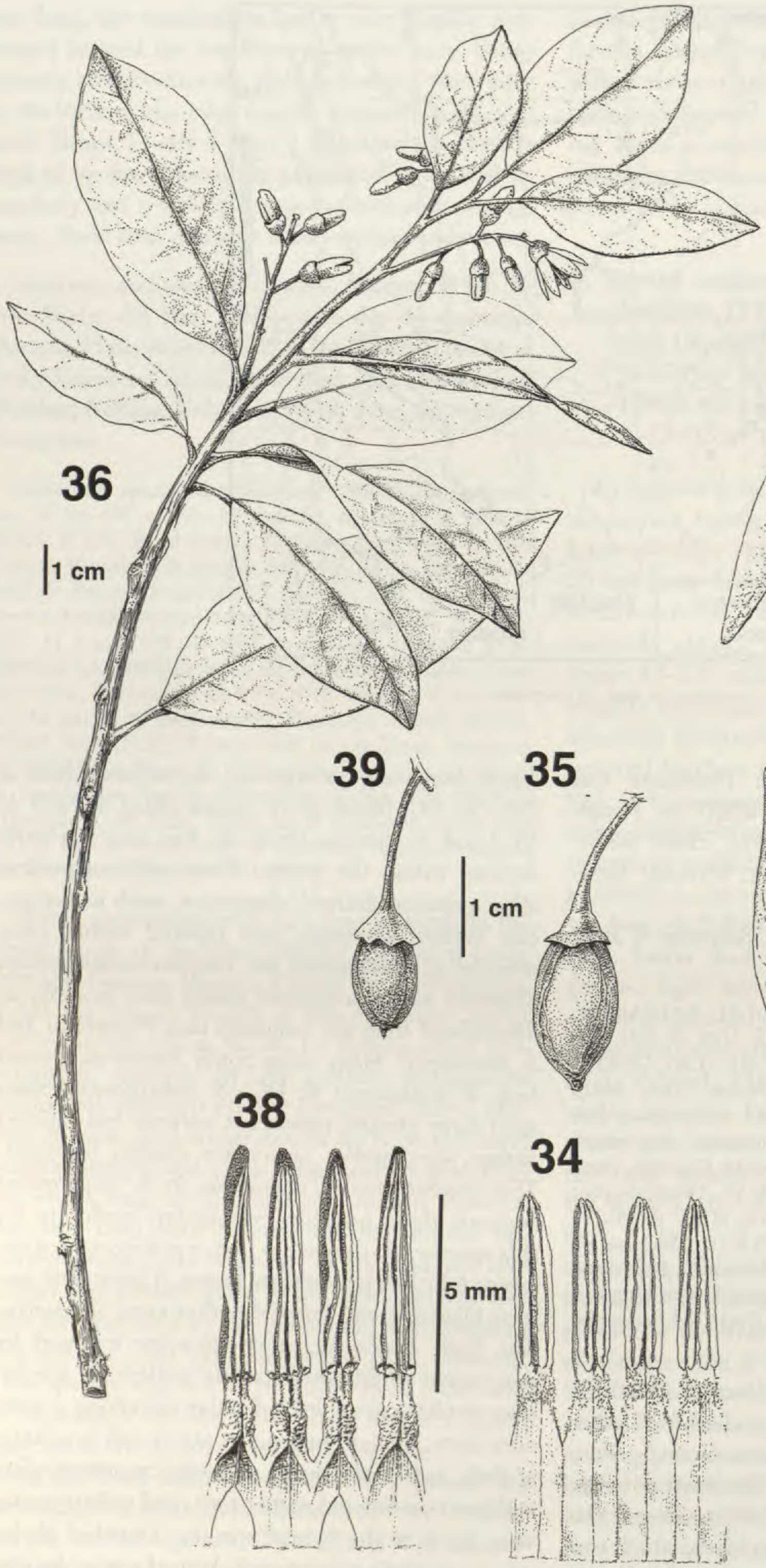
Common names. Copalillo (El Salvador, 4 June 1976, *Reyna s.n. p.p.*).

Additional specimens examined. EL SALVADOR. **Santa Ana:** Cerro Montecristo, *Allen 7184* (F, GH, LL, MICH, US), 4 June 1976, *Reyna s.n. p.p.* (CR). GUATEMALA. **Huehuetenango:** above Puente Alto, *Sharp 45107* (*451047*) (F, GH, MEXU, MO, NY); above San Juan Ixcoy, Sierra de los Cuchumatanes, *Steyermark 49982* (F, US). **Zacapa:** slopes of Volcán Gemelos, *Steyermark 43279* (A, F, NY). HONDURAS. **Ocotepeque:** Alrededor de la Laguna Verde, 12 km al SE de Nueva Ocotepeque, *Darío 59* (DUKE). MEXICO. **Chiapas:** on ridge NE of Cerro Boquerón on road from El Rosario to Niquivil, *Breedlove 68928* (CAS); Niquivil, near Motozintla, *Matuda 15507* (CAS, F, LL, NY); Cerro del Boquerón, *Purpus 7422* (GH, NY).

Styrax conterminus is a rare endemic to northern Mesoamerica. It is easily distinguished from other species within its range by the possession of peltate or lacerate-margined scales on the leaves, twigs, and inflorescences. The only other species in the region with this feature is *S. peruvianus,* which can be distinguished by its auriculate stamen filaments and proportionally broader leaves.

This species possesses an unusual combination of character states. The presence of peltate scales is a feature shared with *Styrax peruvianus* and other South American species, e.g., *S. cordatus* (Ruiz & Pav.) A. DC. [likely = *S. ovatus* (Ruiz & Pav.) A. DC.] and *S. leprosus* Hook. & Arn. and is clearly derived within the genus. These species possess other putative derived characters, such as auriculate stamen filaments and tapered anther sacs, whereas *S. conterminus* has non-auriculate stamen filaments and non-tapered anther sacs (polarity as determined from the outgroup taxa *Pamphilia* and *S. foveolaria*). Many other South American species (e.g., *S. guianensis* A. DC., *S. subargenteus* Sleumer) have stellate-pubescent calyces but tapered anther sacs and/or auriculate stamen filaments. This combination of characters in *S. conterminus* suggests three possible evolutionary pathways for this species: (1) derivation from a peltate-scaled ancestor followed by multiple losses of auriculate stamen filaments and tapered anther sacs; (2) derivation from a non-auriculate ancestor followed by convergent evolution of peltate scales; (3) speciation resulting from hybridization involving a non-auriculate, stellate-pubescent taxon and a peltate-scaled, auriculate taxon, whereby non-auriculate anthers, non-tapered anther sacs, and peltate scales were fixed in the hybrid species. Detailed phylogenetic analysis using morphological and molecular characters would help to determine the likelihood of each of these possibilities.

The protologue of *Styrax conterminus* does not specify the holotype location. Gonsoulin (1974) in-



Figures 33–39. 33–35. *Styrax conterminus*. —33. Leaf. —34. Four adjacent stamens. 33, 34, *Sharp 45107* (= *451047*; F). —35. Fruit, *Allen 7184* (MICH). 36–39. *Styrax peruvianus*. —36. Flowering branch. —37. Flower. —38. Four adjacent stamens. 36–38, *Croat 37190* (MO). —39. Fruit, *I INBio 16* (MO).

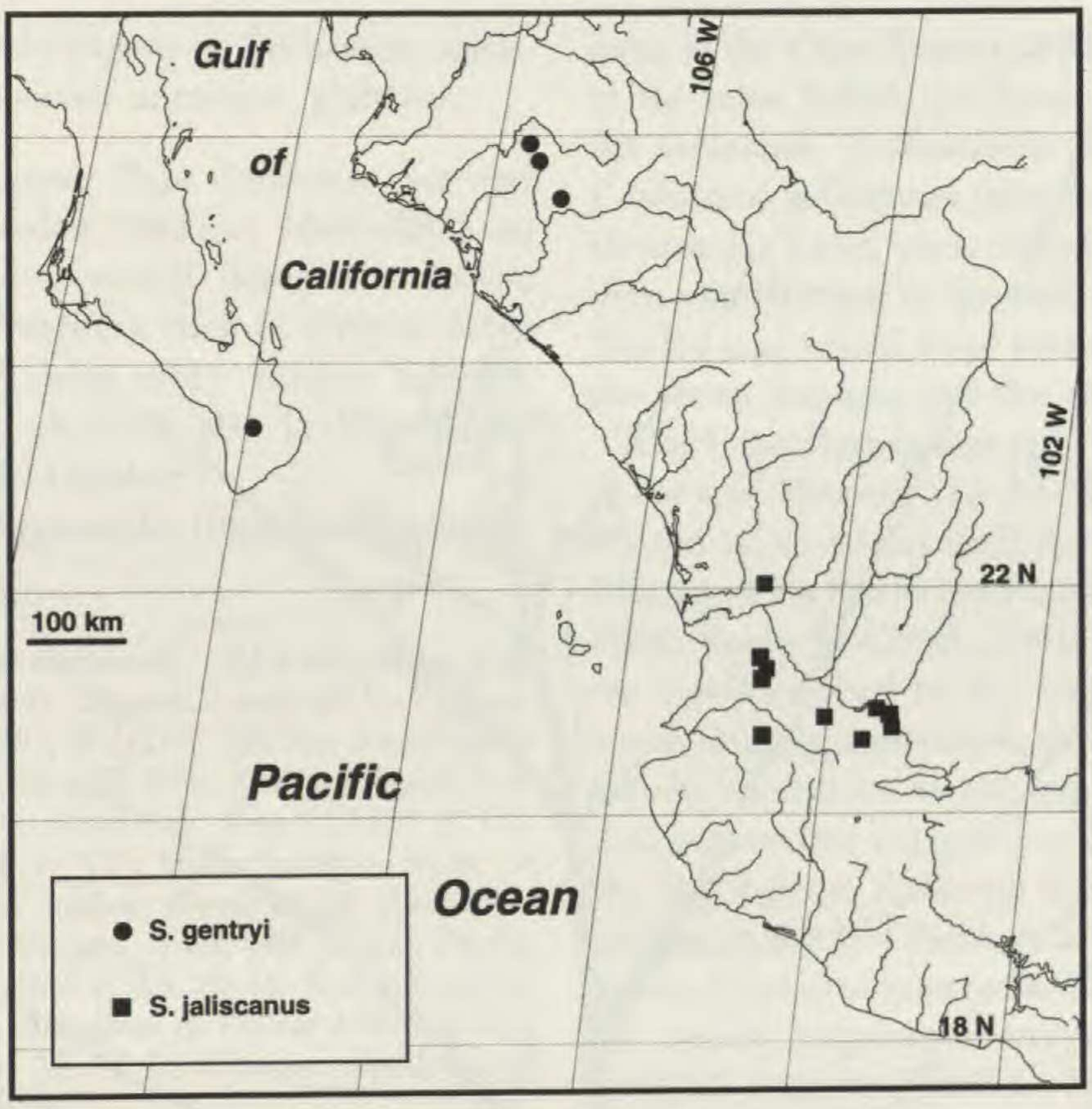


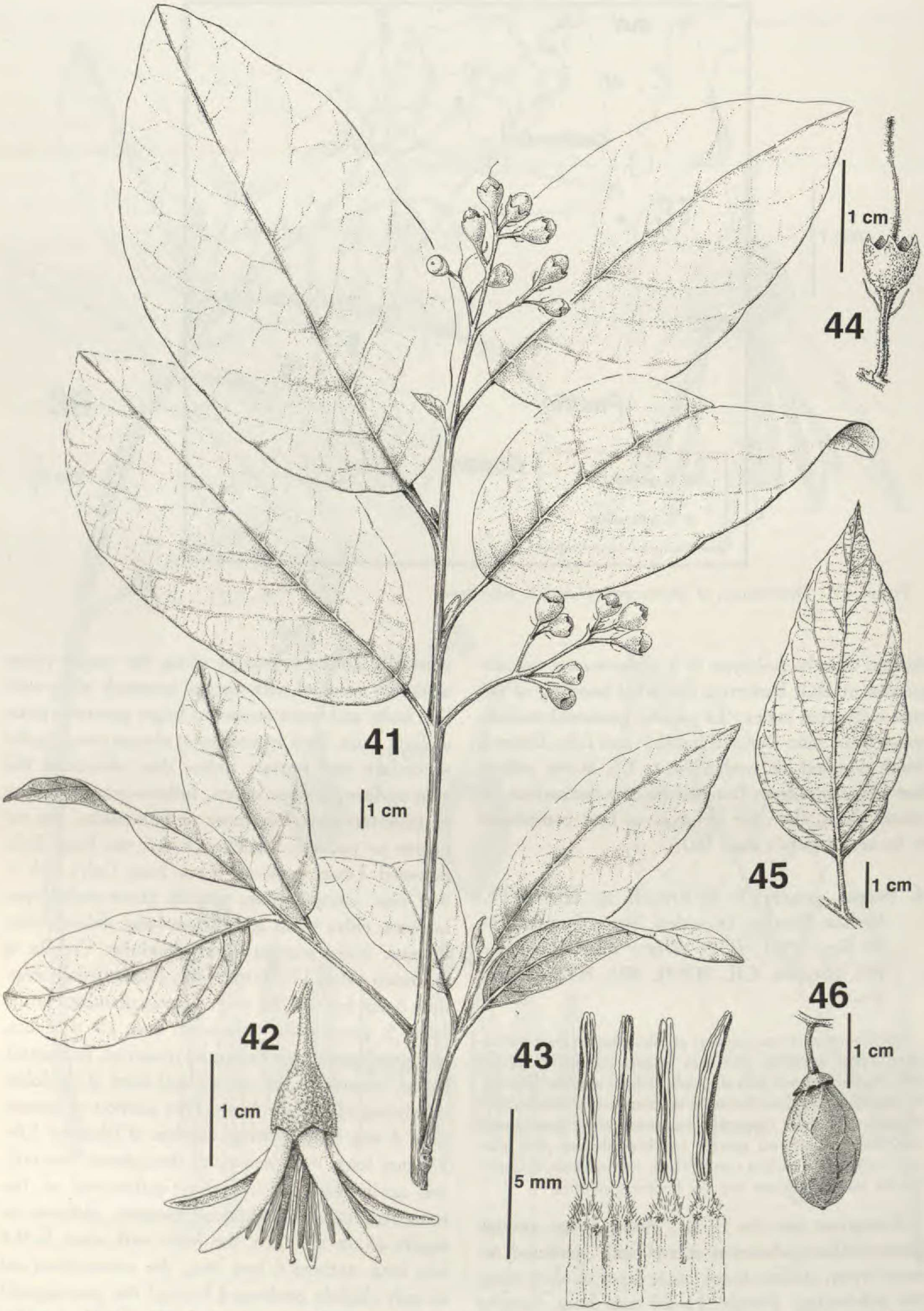
Figure 40. Distribution of *Styrax gentryi* and *S. jaliscanus*.

dicated that the holotype of *S. conterminus* was deposited at MO. However, the label heading of the type collection states "Ex plantis guatemalensibus, quas edidit John Donnell Smith," and John Donnell Smith donated his herbarium to US. If the collection originated from Donnell Smith's herbarium, as seems likely, then the holotype is best considered to be at US rather than MO.

4. **Styrax gentryi** P. W. Fritsch, sp. nov. TYPE: Mexico. Sinaloa: Ocurahui, Sierra Surotato, 1–10 Sep. 1941, *H. S. Gentry 6244* (holotype, DS; isotypes, GH, MICH, MO, NY). Figures 40–44.

Arbor sempervirens; *lamina* subtus alba-stellata-pubescens; *calyx* dentibus 1–2 mm longis, contiguis; *corolla* lobis in aestivatione valvatis, sub anthesi apertis; *filamenta* staminum partibus distinctis ad margines ventrales pilis stellatis aequiliter dispersis instructa, aliter fere glabra ventraliter praeter ad apices, brachis pilorum plus minusve radiatis ex axibus centralibus; *connectivum* antherae loculos non-contractos non vel leviter superans.

Evergreen tree to 17 m. Young twigs grayish green-stellate-pubescent mixed with scattered orange-brown stellate hairs; outer layer of older twigs not exfoliating. Petiole 11–18 mm long. Lamina chartaceous, 13–18 × 6–8 cm, ovate, broadly elliptic, or slightly oblanceolate, secondary veins 16–20; apex acuminate to abruptly acuminate; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute greenish white stellate hairs and more scattered larger greenish white stellate hairs, both types almost always covering the secondary and tertiary veins, thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 3–6.5 cm long, 2–7-flowered. Lower pedicels 6 mm long. Calyx 6–8 × 5–7 mm, campanulate, whitish green-stellate-pubescent; calyx teeth 5, 1–2 mm long, deltoid, contiguous, inner margin often glandular. Corolla of unknown color, 17–20 mm long, petals usually connate 3 mm beyond the calyx margin distally; corolla lobes 5, presumably valvate in bud, 15 × 2 mm, non-overlapping, spreading or recurved, thickened, linear, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 4 mm long; distinct portion of filament 1.0–1.4 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face, the hairs with arms to 0.4 mm long; anthers 6 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3 mm wide. Largest drupe observed (only immature fruits available for study) 10 × 7 mm, ellipsoid; wall ir-



Figures 41–46. 41–44. *Styrax gentryi*. —41. Fruiting branch, *Gentry 6244* (vegetative; MO) and *Breedlove 15588* (infructescence; F). —42. Flower. —43. Four adjacent stamens. 42, 43, *Domínguez 28* (HCIB). —44. Calyx, *Gentry 6244* (MO). 45, 46. *Styrax tuxtlensis*. —45. Leaf, *LaFrankie 1306* (CAS). —46. Fruit, *LaFrankie 1306* (MO).

regularly and coarsely rugose on herbarium specimens. Seed coat observed immature, glabrous.

Sierra de La Laguna, Baja California Sur and Sierra Surotato, Sinaloa, Mexico; 1600–2200 m; *Quercus-Pinus* forest, mixed dominants forest; found in riparian situations, such as arroyos, steep moist ravines, and deep rocky canyon bottoms. Flowering: October, probably also in March, August; fruiting: March, October

Common name. Aguacatillo (Baja California Sur, *Domínguez 28*).

Additional specimens examined. MEXICO. **Baja California Sur:** Sierra de la Laguna, Arroyo de los Encinos Blancos, *Domínguez 28 ("R.D.C.")* (HCIB); Sierra de la Laguna, *Gentry 4420* (DS, GH, MO). **Sinaloa:** Sierra Surotato, near Los Ornos, *Boutin & Brandt 2878* (CAS), *Breedlove 15588* (CAS, F, NY); Sierra Surotato, Mpio. de Badiraguato, Ocurahui valley, *Breedlove & Kawahara 16893* (CAS); Sierra Surotato, 5 mi. NW of Los Ornos, *Breedlove & Thorne 18269* (CAS, RSA); Sierra Surotato, 3 mi. N of Los Ornos, *Breedlove & Thorne 18414* (CAS); Sierra Surotato, 5 mi. NE of La Ciénega, *Breedlove & Thorne 18584* (CAS, RSA).

Styrax gentryi is a rare species with a disjunct distribution in the Sierra de la Laguna of Baja California's Cape Region and the Sierra Surotato in northwestern Sinaloa, Mexico. It is particularly appropriate that the species be named after Howard Scott Gentry (1903–1993), considering that he was able to collect this plant in both disjunct localities—from Baja California Sur in 1939 (the first collection of the species) and Sinaloa in 1941.

This species is easily distinguished from all other species of evergreen *Styrax* by the prominent calyx teeth, evident even in fruit. This is one feature that probably led Gonsoulin (1974) to include *Gentry 6244* and *Gentry 4420* within the deciduous capsular-fruited species *S. jaliscanus*. These collections were made just after anthesis, so no flowers or fruits are available for examination. However, a third collection (*Breedlove 15588*) with the same calyces and leaves as the Gentry collections is annotated as *S. argenteus* var. *argenteus* by Gonsoulin. This collection has immature fruit that establishes its affinity with the evergreen, drupe-bearing species rather than the deciduous, capsule-bearing species. A relatively recent flowering collection (*Domínguez 28*) further confirms the affinity of this species with the evergreen taxa by virtue of its nonoverlapping corolla lobes.

This species's disjunct distribution seems not to be strictly paralleled in other flowering plants, although distribution patterns of at least two species are similar: *Populus monticola* Brandegee and *Ilex tolucana* Hemsl. both occur in the Sierra de la Laguna of the Cape Region of Baja California Sur and in the same habitat as *Styrax gentryi*. However, on the mainland, *P. monticola* occurs in Sonora, and *I. tolucana* is disjunct from Sonora to Veracruz and Oaxaca (L. Lenz, pers. comm.). Additional collections contributing to the still poorly known flora of Sinaloa may reveal more taxa that are disjunct from the Sierra Surotato and the Sierra de la Laguna.

The Cape Region first split from northern Jalisco in the mid-Miocene (13–14 Mya; Smith, 1991) and existed as an island until the establishment of the Isthmus of La Paz in the Pleistocene (López Ramos, 1983; Fenby & Gastil, 1991). Because the two areas circumscribed by the range of *S. gentryi* were never directly connected, explaining this disjunction by vicariance would require a prior mainland distribution that extended at least partly into Nayarit and Jalisco. Although the narrow range of this species in the two disjunct areas suggests relictual status, *S. gentryi* is presumably bird-dispersed and the current mainland distribution does not extend south of northern Sinaloa. Thus, dispersal across the Gulf of California remains a viable explanation. Genetic analysis of disjunct populations of *S. gentryi* and additional information regarding its distribution and ecology would help to clarify this biogeographic issue.

5. Styrax glabratus Schott, in Spreng., Syst. veg. 4(2): 406. 1827. *Strigilia glabrata* (Schott) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 283. 1859. TYPE: Brazil. Rio de Janeiro: *Sellow 807* (holotype, ?BP; isotypes, F, US (2)). Figure 47.

Styrax erymophyllus Pohl ["*S. erymophyllum*"], Pl. bras. icon. descr. 2: 57. 1830. TYPE: Brazil. Rio de Janeiro: *Schott 4184* (holotype, W; isotypes, BR(2), F, GH, W(3)).

Epigenia integerrima Vell., Fl. flumin. 183. 1829. TYPE: Icon. 4, t. 137 in Vell., Fl. flumin., 1831 (holotype).

Styrax psilophyllus A. DC., Prodr. 8: 266. 1844 ["*S. psilophyllum*"]. *Strigilia psilophylla* (A. DC.) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 283. 1859. TYPE: French Guiana. Cayenne, *Martin s.n.* (holotype, P; isotype, US).

Styrax leiophyllus Miers, in Lindl., Veg. kingd. Ed. 3: 593a, t. 402 p.p. 1853 ["*S. leiophyllum*"]. *Strigilia leiophylla* (Miers) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 283. 1859. TYPE: Brazil. Rio de Janeiro: Valença, *John 1345* (holotype, BM not seen; photo of holotype, NY).

Styrax lauraceus Perkins, Bot. Jahrb. Syst. 31: 478. 1902. TYPE: Venezuela. Distrito Federal: Galipan, *Karsten 41* (holotype, B destroyed; photo of holotype, NY(2); isotype, F).

Styrax squamulosus M. F. Silva, Acta Amazon. 1: 23. 1971 ["*S. squamulosa*"]. TYPE: Brazil. Amazonas: Manaus, Reserva Florestal Ducke, 1390 Levantamento,

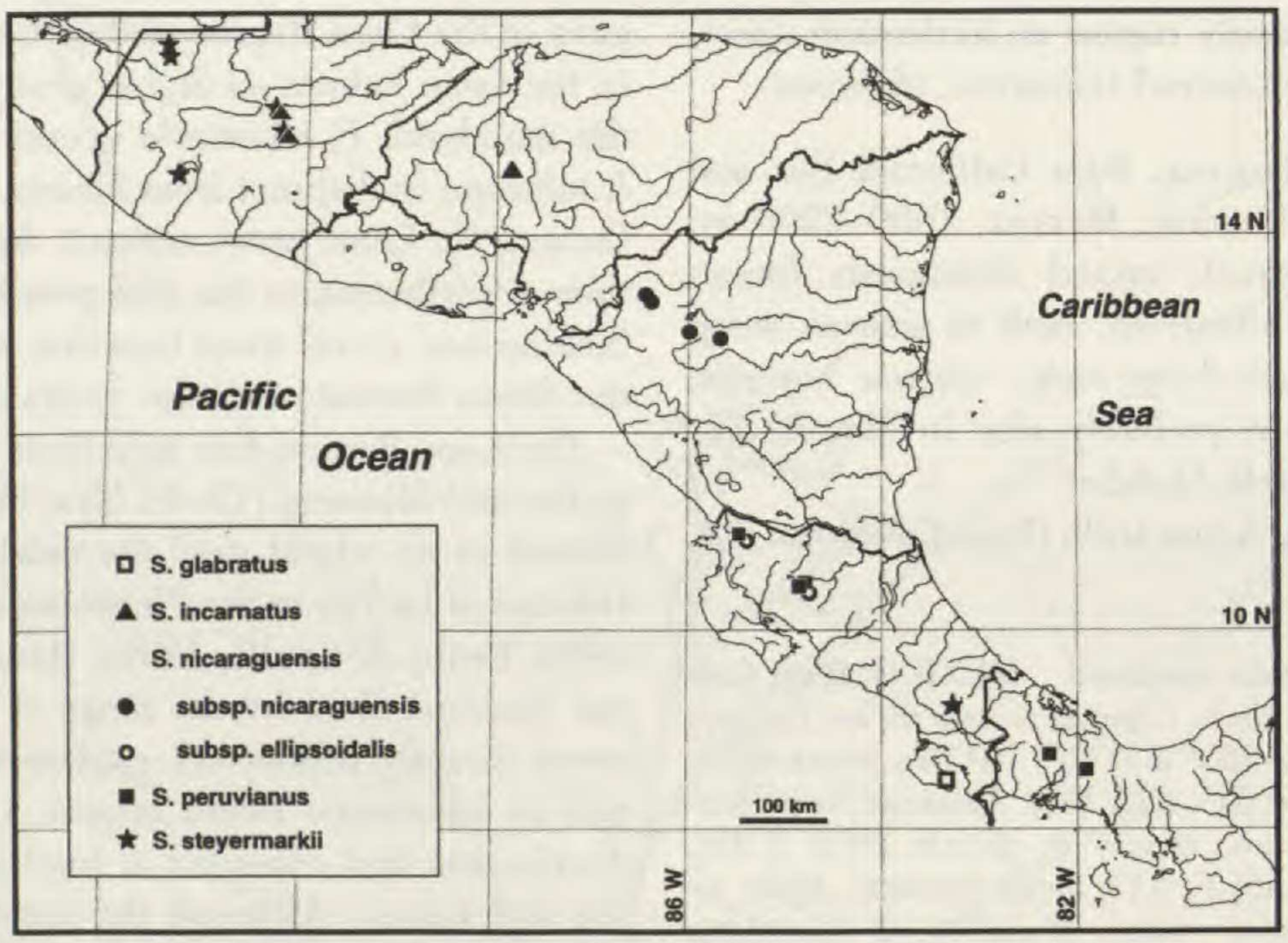


Figure 47. Distribution of *Styrax glabratus*, *S. incarnatus*, *S. nicaraguensis* subsp. *nicaraguensis*, *S. nicaraguensis* subsp. *ellipsoidalis*, *S. peruvianus*, and *S. steyermarkii*.

14 Mar. 1971, *W. Rodrigues & D. Coêlho 8342* (holotype, INPA not seen; isotype, NY).

Evergreen tree to 20 m. Young twigs sparsely to densely greenish gray-stellate-pubescent or radiate-lepidote; outer layer of older twigs not exfoliating. Petiole 5–16 mm long. Lamina subchartaceous, 9–19 × 2.5–6 cm, 2.2–3.8(–5.2) times as long as wide, elliptic or oblanceolate, secondary veins 6–9; apex acute to acuminate; base cuneate, symmetric or slightly oblique; adaxially glabrous or sparsely pubescent on the midvein at the base; abaxially glabrous except for the midvein at the base, or rarely sparsely stellate-pubescent or radiate-lepidote, occasionally with domatia in the axils of the secondary veins, the hairs white to grayish green; margin entire. Inflorescences axillary or false-terminal, racemose or rarely paniculate, the racemes or panicle branches 2–7 cm long, (1)2–8-flowered. Lower pedicels 2–13 mm long. Calyx 4–7 × 4–6 mm, cupuliform, usually grayish green-radiate-lepidote (always in Costa Rica), sometimes with a few orange-brown radiate scales toward the base, rarely (SE Brazil) stellate pubescent; scales at mid-calyx 0.13–0.29 mm diam.; calyx teeth 5 or often absent, to 0.5 mm long, linear-deltoid, the calyx margin truncate between the teeth, inner margin eglandular. Corolla white to pale pink, 13–20 mm long, petals connate 1–4 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 8–13 × 2.5–3 mm, non-overlapping, reflexed, slightly thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of radiate scales or stellate hairs. Free portion of stamen tube 2–2.5 mm long; distinct portion of filament 1.5–2 mm long, somewhat incurved, of equal width throughout, ventrally not auriculate, each margin with a cluster or longitudinal line of stiff white stellate hairs, these sometimes also occurring on the ventral face, the hairs with arms to 1.8 mm long, the hairs nearest the distal end of the filament with arms predominantly directed upward; anthers 5–8 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely short-stellate-pubescent; style glabrous; stigma 0.3–0.4 mm wide. Drupe 13–18 × 7–9 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens; fruiting calyx funnelform, 4–8 mm long. Seed coat glabrous.

Osa Peninsula, SW Costa Rica; also Colombia, Venezuela, Suriname, French Guiana, and Brazil; 400 m in Costa Rica. Flowering: October (buds) in Costa Rica.

Specimens examined. COSTA RICA. **Puntarenas:** Cantón de Golfito Jiménez, Río Piro camino a Cerro Osa, *Herrera 4534* (CR, INB).

In North America, *Styrax glabratus* has thus far been documented only from the Osa Peninsula in Costa Rica; the major portion of its range is in South America, from Colombia to southeastern Brazil. The existence on the Osa Peninsula of a species otherwise found only in South America is not discordant with the general composition of the Osa flora, which comprises many endemics and species otherwise not known in Costa Rica and has strong affinities to the flora of the Chocó region in Colom-



Figure 48. Distribution of *Styrax glabrescens*.

bia (Hartshorn, 1983; Grayum & de Nevers, 1988). In South America, the species is most commonly found close to the margins of the continent in restingas, pluvial forests, and moist evergreen forests, but in northern South America it extends as far inland as Manaus, Brazil, where it occurs in terra firme forests on clay.

The species is easily distinguished from other species in Costa Rica by its evergreen habit, glabrous abaxial laminar surface, and drupaceous fruit. The lamina of *Styrax glabrescens* is also nearly to completely glabrous abaxially and adaxially, but that species is deciduous and has a dry fruit. Rarely *S. warscewiczii* has nearly glabrous abaxial laminar surfaces as well, but it has smaller leaves, usually occurs above 1500 m elevation, and the ventral side of the stamen filaments has hairs with short arms (to 0.3 mm long).

In Espirito Santo and extreme southern Bahia, Brazil, the calyx of *S. glabratus* is stellate-pubescent, not radiate-lepidote as is otherwise the case. Plants of *S. glabratus* with this feature will key to *S. argenteus* in the present treatment. *Styrax argenteus* can be distinguished from *S. glabratus* by the possession of densely stellate-pubescent abaxial leaf surfaces and the presence of small auricles partly hidden by the hair mass at the margins of the stamen filaments; the leaf of *S. glabratus* is glabrous or nearly so on both sides and the stamen filaments lack auricles.

An additional collection from the Osa Peninsula (*Aguilar 4140*) is also reportedly *S. glabratus*.

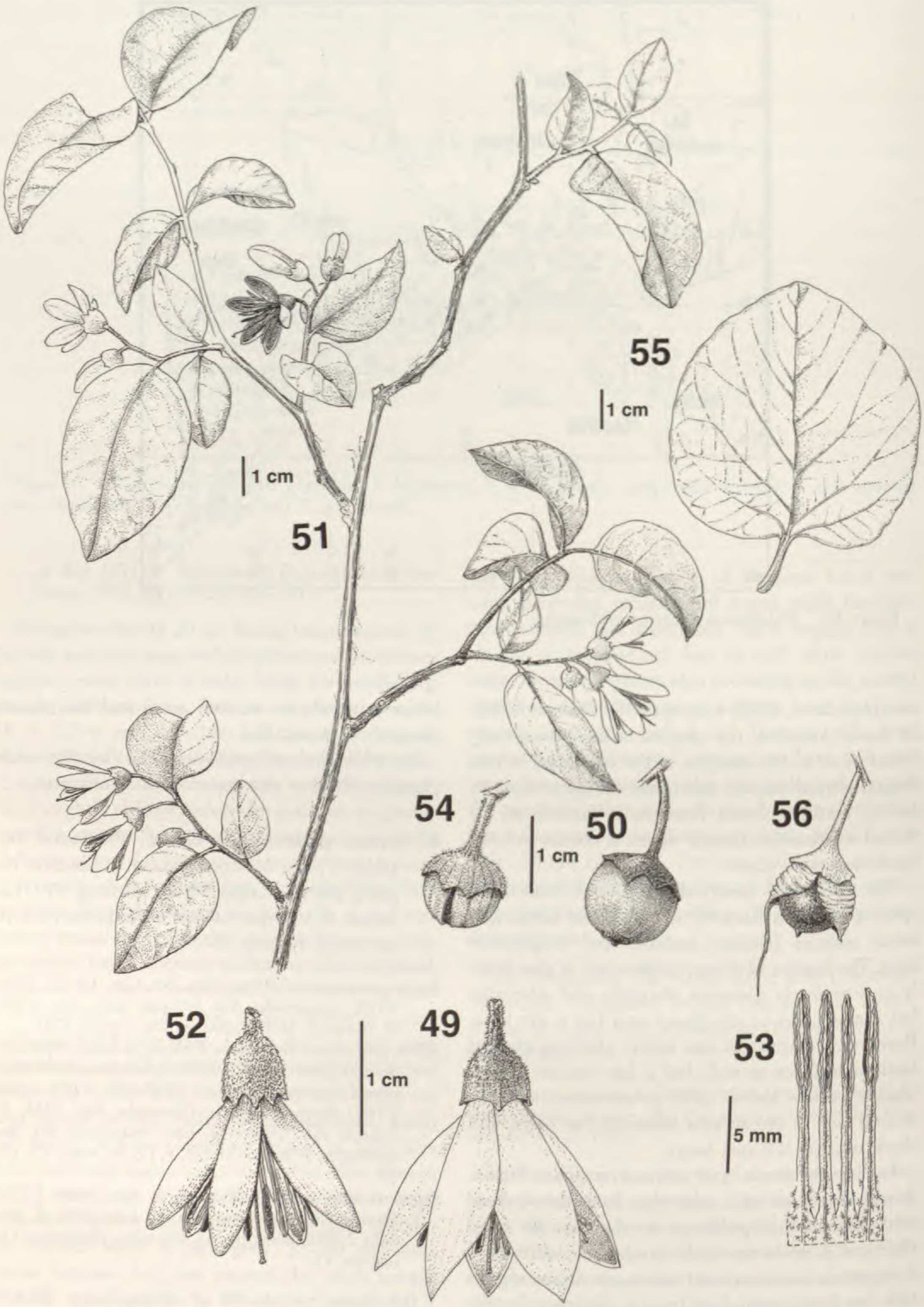
6. Styrax glabrescens Benth., Pl. hartw. 66. 1840. TYPE: Mexico. Oaxaca: [Chinantla region], planitie Llano Verde, *Hartweg 489* (holotype, K; isotype, LD not seen, photo in XAL not seen). Figures 48–50.

Styrax guatemalensis Donn. Sm., Bot. Gaz. 15: 27. 1890. TYPE: Guatemala. Alta Verapaz: Sasis, Apr. 1889, *H. Helmrich 1690* (holotype, US; isotype, GH).

Styrax glabrescens var. *pilosus* Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 72. 1907. *Styrax pilosus* (Perkins) Standl., Contr. U.S. Natl. Herb. 23: 1129. 1924. TYPE: Mexico. Oaxaca: Chinantla, May 1844, *H. Galeotti 2852* (lectotype, here designated, BR; isolectotypes, B destroyed, BR, F, LE not seen, NY, US, W).

Styrax vestitus Lundell, Wrightia 4: 121. 1969. TYPE: Mexico. Chiapas: Concordia, 16 June 1945, *E. Matuda 15922* (holotype, LL not seen, photocopy, LL; isotype, F).

Deciduous tree to 30 m. Young twigs densely whitish or yellowish stellate-pubescent or nearly glabrous, often with scattered orange-brown or dark brown stalked stellate hairs toward the base; outer layer of older twigs often exfoliating into long strips.



Figures 49–56. 49, 50. *Styrax glabrescens.* —49. Flower, *Calzada 4333* (F). —50. Fruit, *Cházaro 1511* (F). 51–54. *Styrax jaliscanus.* —51. Flowering branch. —52. Flower. —53. Four adjacent stamens. 51–53, *Pringle 11012* (F). —54. Fruit, *Breedlove 61642* (CAS). 55, 56. *Styrax platanifolius* subsp. *youngiae, Henrickson 11561* (TEX). —55. Leaf. —56. Fruit.

Petiole 6–16 mm long. Lowest leaf pair on each twig often subopposite or opposite. Lamina membranous, 3.5–14 × 1.5–10 cm on fertile branches [sometimes smaller and nearly bract-like; laminae of sterile branches nearly always larger (to 21 × 11 cm)], ovate or obovate, sometimes (especially the terminal leaf on sterile twigs) rhombic or suborbicular, secondary veins 6–8; lowest leaf pair often ovate-oblong; apex cuspidate to long-acuminate; base narrowly cuneate to rounded, rarely truncate or attenuate, symmetric or slightly oblique, the bases of lowest two leaves often oblique; adaxially glabrous except along the major veins; abaxially covered with white stellate hairs or more often glabrous or nearly so, often with scattered orange-brown or dark brown stalked stellate hairs especially prevalent on veins and the lowest pair of leaves on each shoot, the stellate portion often deciduous from the base, the veins glabrous or moderately pubescent; margin serrate or entire but always glandular, the teeth tipped by the glands. Inflorescences racemose or rarely paniculate, axillary or false-terminal, axillary racemes usually present, 1–5(–17)-flowered, shorter than the false-terminal raceme and occurring in the leaf axils immediately below it, sometimes more than one raceme occurring in the same leaf axil, false-terminal racemes 2–10.5 cm long, (1)2–12(–21)-flowered. Lower pedicels 3–10 mm long. Calyx 4–6 × 4–6 mm, campanulate or broadly cupuliform, grayish green-stellate-pubescent, often also with various amounts of yellow, orange-brown, or dark brown stellate hairs especially toward the base, more thinly pubescent within 1 mm from apex; calyx teeth 0–7, unevenly distributed, to 0.8 mm long, narrow-deltoid or linear, contiguous or separated by the truncate or slightly concave calyx margin, inner margin eglandular. Corolla white, 14–28 mm long, petals connate 0–2 mm beyond the calyx margin distally; corolla lobes 5(–10), imbricate in bud, 11–23 × 6–10 mm, overlapping, spreading, thin, elliptic or broadly elliptic, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube none; distinct portion of filament 6–9 mm long, of equal width throughout or narrowing distally, ventrally not auriculate, moderately densely white-stellate-pubescent on the face, becoming glabrous distally, the hairs with arms to 0.2 mm long; anthers 4–6 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary thinly or densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3–0.6 mm wide. Fruit 10–15(–17) × 9–15(–19)(wider when 2-seeded) mm, globose, indehiscent (rarely 3-valve-dehiscent), hard-walled; wall smooth (but stellate-pubescent). Seed coat glabrous.

Querétaro and northern Veracruz, Mexico, to southwestern Costa Rica; common on the eastern slopes of the Sierra Madre Oriental, becoming scattered southward to Nicaragua, but frequent on the Pacific slope of the cordillera in Costa Rica; 500–2600 m; evergreen cloud forest, temperate deciduous forest, montane rainforest of oak-pine, elfin forest, subdeciduous forest, bosque mesofilo de montaña; found frequently along waterways, also on steep slopes; in soil of high organic content or clay, often with rocks, in primary or secondary growth. Flowering: commonly December–May, rarely June, July; fruiting: throughout much of the year, but most commonly maturing April–September.

Common Names. Azucena (Guatemala, *Steyermark 49738*); jazmincillo (Veracruz, *López & Sosa 503*), palo blanco (Chiapas, *Calzada et al. 8791*; Querétaro, *Servín 15*), salamo (El Salvador), zapotillo (Veracruz, *Cházaro 1511* and *2691*); from Pacheco (1983): azahar del monte, cucharillo, flor de azahar, jazmín, zapotillo (Veracruz).

Uses. Firewood (Guatemala, *Steyermark 49738*).

Selected specimens examined. COSTA RICA. **Alajuela:** Reserva Forestal de San Ramón, valley of the Río Lorencito, *Burger et al. 12475* (CAS, DUKE, F). **Cartago:** near Río Patarrá, 2 km S of Muñeco, *Lent 1932* (AAU, CR, DUKE, F, MEXU, MO, NY). **Puntarenas:** around Río Canasta, 9.5 km NW of Agua Caliente, *Davidse et al. 28381* (CR, F, MO, TEX). **San José:** Pacific slope of Chirripó massif, *Davidse & Pohl 1656* (DUKE, MO, NY). EL SALVADOR. **Santa Ana:** Cerro Montecristo, 20 May 1976, *Reyna s.n.* (CR). GUATEMALA. **Alta Verapaz:** region of Cocolá, NE of Carchá, *Standley 70316* (F). **Baja Verapaz:** Niño Perdido, between km 151/152W, *Lundell & Contreras 21126* (CAS, LL, MEXU, MO, NY). **Huehuetenango:** Barillas, *Holdridge 2338* (F, US); Cerro Victoria, Sierra de los Cuchumatanes, *Steyermark 49738* (F). **Quezaltenango:** La Shuya, SW of San Martín Chile Verde, *Standley 67865* (F). **Quiché:** valley of Río de las Violetas, N of Nebaj, *Proctor 25210* (F, LL, MO). **San Marcos:** Volcán Tajumulco, 9 mi. S and W of Tajumulco, *Steyermark 36807* (F). **Suchitepéquez:** Volcán Santa Clara, *Steyermark 46750* (F). HONDURAS. **Comayagua:** near the summit of the range above El Achote, *Yuncker et al. 6175* (F, GH, MO, NY, U). **La Paz:** Montaña Verde on Cordillera Guajiquiro, *Molina & Molina 24404* (DS, F, NY). **Lempira:** 8.8 km al SE de Gracias, Parque Nacional de Celaque, *Darío 72* (DUKE). **Olancho:** along Río Olancho, 13.6 mi. SW of Gualaco, *Croat 64211* (DUKE). **Yoro:** Río Pijol Valley, 6 to 7 km S of Nueva Esperanza, *Liesner 26612* (DUKE). MEXICO. **Chiapas:** on the SE side of Cerro Tres Picos, *Breedlove 34377* (F, DS, DUKE, LL, MEXU, MICH, MO, NY, POM). **Guerrero:** 25 km al NE de Paraíso, *Núñez et al. 5243* (F, MEXU, MO). **Hidalgo:** river bluffs below Trinidad Iron Works, *Pringle 13104* (BH, CAS, F, GH, MICH, MO, US). **Oaxaca:** Dto. de Ixtlán, Mpio. de Comaltepec, *Martin 501* (CAS, MEXU, MO, NY, US). **Puebla:** Mpio. de Hueytamalco,

Colijuit, *Ventura 784* (DS, F, MICH, MO, US). **Querétaro:** 1.5 km al SE de La Yesca, *Rubio 1711* (MICH, MO, TEX). **San Luis Potosí:** Cerro de la Silleta, Cerca de Zilitla, *Paray 681* (MEXU, MICH). **Tamaulipas:** Sierra de Guatemala, *Sullivan 543* (DUKE, MO, NY, TEX). **Veracruz:** Rancho La Martinica, a 5 km al N del pueblo de Banderilla, *Calzada 4333* (F, MEXU); entre Coatepec y Coatepec Viejo, *Cházaro 1511* (F); hills near Jalapa, *Pringle 8129* (A, B, BH, BR, F, GH, MO, NY, POM, US, W). NICARAGUA. **Zelaya:** along trail from Cerro El Inocente toward Cerro Saslaya, *Stevens 6687* (MO).

Styrax glabrescens is one of the most common and widespread species of *Styrax* in the present revision, occurring from northeastern Mexico to southern Costa Rica. It appears to be most abundant in the cloud forests of central Veracruz, Mexico. It is the only deciduous member of the genus in the region with a tree habit; *S. platanifolius* and *S. jaliscanus* are shrubs that are multi-stemmed from the base. *Styrax glabratus* might at first be mistaken for *S. glabrescens* on the basis of its glabrous abaxial laminar surface, but it is evergreen and has a drupe instead of a dry fruit.

Perkins (1907) differentiated *Styrax glabrescens* var. *pilosus* from the typical variety on the basis of the dense pubescence on the lower laminar surface. Standley (1924) raised this taxon to the rank of species solely on this basis. Gonsoulin (1974) agreed with Perkins (1907), but in addition to the difference in leaf pubescence he distinguished variety *pilosus* from variety *glabrescens* by describing the calyx of variety *pilosus* as minutely grayish tomentulose, as opposed to rufous or yellowish pilose-stellate in variety *glabrescens.* Pacheco (1983) agreed with Standley, citing the leaf pubescence difference as well as the length of the inflorescence, the number of flowers, and the glaucous aspect of the leaves (on the lower laminar surface?) as justification for the delimitation of two species.

In my analysis of the problem I have found no basis for recognizing either two species or two varieties within *Styrax glabrescens.* The pubescent form of *S. glabrescens* has a distribution largely overlapping that of the glabrous form, occurring from Tamaulipas, Mexico, at the extreme northern edge of the species' range, south to Guatemala, whereas the glabrous form occurs throughout the range of the species. The pubescent form also exhibits no obvious elevation or habitat distinction, and seems to occur sporadically, often near collection localities of the glabrous form. Furthermore, several collections show an intermediate amount of pubescence between the types of *S. glabrescens* var. *pilosus* and variety *glabrescens.* Similar variation in pubescence amount without concomitant geographic distinction or ecological separation occurs in *S. grandifolius,* and that species was not treated as having varieties by Perkins (1907) or Gonsoulin (1974). *Styrax redivivus* in California also shows the same type of pubescence variation, but despite additional characters associated with the pubescence differences, varietal status on this basis was not considered warranted because the variation is distributed clinally (Fritsch, 1996b). To be taxonomically consistent, and considering the weak to nonexistent geographical and ecological bases for distinguishing either two species or two varieties within *S. glabrescens,* I have subsumed *S. glabrescens* var. *pilosus* (= *S. pilosus*) under *S. glabrescens.*

The protologue of *Styrax glabrescens* indicates a type collection date of April–July 1839. Gonsoulin (1974) incorrectly cited the type of *S. glabrescens* as "*Linden,* Jun 1838" at K.

A collection date of May 1844 is indicated on the lectotype of *S. glabrescens* var. *pilosus* (*Galeotti 2852*) [as well as on some of the isotypes of *S. cyathocalyx* (*Galeotti 1687*); see under *S. ramirezii*]. However, Galeotti had left Mexico by 1840 (McVaugh, 1978) and seems not to have returned. Early in the year of 1840 he was presumed to have visited northeast Oaxaca, where the *2852* collection was made. If a transcription error occurred on the *2852* labels, then it is likely that the collection was made in 1840. I have found no additional information that explains the discrepancy. Some type specimens of *S. glabrescens* var. *pilosus* are designated "*3852*" and are presumably the result of a transcription error.

In the protologue of *Styrax glabrescens* var. *pilosus,* Perkins (1907) specifically listed two specimens of the type collection *Galeotti 2852:* B and BR; thus, these are technically syntypes and a lectotypification of this name is in order. Because the B specimen has been destroyed, I have chosen the two BR sheets (here interpreted as constituting a single specimen) as the lectotype.

The collection date of the type of *Styrax vestitus* is 16 June 1945 according to the label information, but 14 June 1945 according to the protologue. Also regarding *S. vestitus,* the collection number of the type is *5922* in the protologue and on the photocopy of the holotype, but *15922* on the F isotype.

7. **Styrax incarnatus** P. W. Fritsch, sp. nov. TYPE: Guatemala. Baja Verapaz: Niño Perdido, La Cumbre de San José Espinero, 20 May 1977, *C. L. Lundell & E. Contreras 20933* (holotype, CAS; isotypes, LL, MEXU, MO, NY). Figures 28–30, 47.

Arbor sempervirens; *lamina* crassi-chartacea, 12–17 × 5.5–9.5 cm longa, ovata vel late elliptica, subtus pilis densis cinerascentibus-viridibus-stellatis et dispersis ferrugineis-stellatis instructa, venis secondariis et tertiariis occultis a tomento; *pedicelli* inferiores 3–9 mm longi; *calyx* 3–3.5 × 2.5–4.5 mm, stellata-pubescens; *corolla* (10–)15–24 mm longa, lobis in aestivatione valvatis, sub anthesi apertis; *filamenta* staminum partibus distinctis ad margines ventrales pilis stellatis aequiliter dispersis instructa, aliter fere glabra ventraliter praeter ad apices, brachis pilorum plus minusve radiatis ex axibus centralibus; *connectivum* antherae loculos non-contractos non vel leviter superans.

Evergreen tree to 21 m. Young twigs dark orange-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 10–17 mm long. Lamina thick-chartaceous, 12–17 × 5.5–9.5 cm, ovate or broadly elliptic, secondary veins 12–15; apex acute to abruptly acuminate; base subrounded to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute greenish white stellate hairs, larger greenish white stellate hairs with arms to about 0.3 mm long, and somewhat larger orange-brown stellate hairs, the latter particularly prevalent near and on the major veins, the minute and larger whitish hairs occurring on the secondary and tertiary veins thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 5–9 cm long, 3–7-flowered. Lower pedicels 3–9 mm long. Calyx 3–3.5 × 2.5–4.5 mm, conical with rounded base, greenish white-stellate-pubescent with somewhat larger scattered orange-brown stellate hairs toward the base; calyx teeth 5, to 0.5 mm long, deltoid, the calyx margin concave between the teeth, inner margin often glandular. Corolla pink or purplish pink, (10–)15–24 mm long, petals connate (2–)4–7 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, (6–)9–16 × 2–4 mm, non-overlapping, nearly erect or moderately spreading, linear, thickened, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube (1–)3.5 mm long; distinct portion of filament (1–)2 mm long, of equal width throughout, ventrally not auriculate, sparsely pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.3 mm long; anthers (4–)5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style with a few hairs at base only; stigma 0.5 mm wide. Largest drupe observed (only immature fruits available for study) 9 × 6 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat observed immature.

Rare, occurring in the departments of Baja Verapaz and Alta Verapaz, Guatemala, and the department of Comayagua, Honduras; 1900 m; "in high forest," cloud forest of mixed hardwood species. Flowering: May, August, November; fruiting: immature fruit in November.

Additional specimens examined. GUATEMALA. **Baja Verapaz:** Unión Barrios, NW of km 159 of the road, *Lundell & Contreras 19450* (LL, MO); Unión Barrios, W of km 159 of the road, *Lundell & Contreras 19618* (CAS, LL). HONDURAS. **Comayagua:** trail to San Juanillo of the Cordillera de Montecillos, *Thomas 26* (DUKE).

Styrax incarnatus is a rare endemic to Guatemala and Honduras. Of the *Styrax* species that grow in Guatemala and Honduras it resembles most closely *S. warscewiczii*, from which it is easily distinguished by its much larger leaves, stellate-pubescent calyx, and usually larger flowers. The species also resembles *S. austromexicanus*, which differs mainly in its narrowly elliptic leaves, shorter pedicels, and smaller calyces.

The sole Honduran collection (*Thomas 26*) has shorter corollas than the Guatemalan collections, but matches them otherwise. More collections, especially those in fruit, would help clarify the degree of character variation, natural history, and evolution of this species.

8. Styrax jaliscanus S. Watson, Proc. Amer. Acad. Arts 26: 144. 1891. *Styrax officinalis* L. var. *jaliscanus* (S. Watson) Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 82. 1907. TYPE: Mexico. Jalisco: Sierra de San Esteban near Guadalajara, 10 Nov. 1889, *C. G. Pringle 2978* (lectotype, here designated, GH; isolectotype, A). Figures 40, 51–54.

Deciduous shrub multi-stemmed from the base, to 2 m. Young twigs densely white-stellate-pubescent, often toward the base with scattered orange-brown or dark brown stalked stellate hairs; outer layer of older twigs often exfoliating into long strips. Petiole 4–5 mm long. Lamina chartaceous, 5–13 × 3.2–8 cm, orbicular, ovate-orbicular, broadly elliptic, or obovate, often slightly conduplicate, as evidenced by the longitudinally folded laminae on herbarium specimens, secondary veins 7–10; apex acute, cuspidate, or abruptly acuminate; base subcuneate or rounded, rarely subcordate, sometimes slightly attenuate, if subcordate then not at all attenuate, symmetric or slightly oblique; adaxially stellate-pubescent; abaxially thickly covered with white stellate hairs, often with scattered orange-brown or dark brown stalked stellate hairs especially prevalent on veins and the lowest pair of leaves

on each shoot, the stellate portion often deciduous from the base, sometimes old leaves more sparsely tomentose, the veins tomentose or nearly glabrous, secondary and tertiary veins prominent; margin serrulate or entire, glandular or eglandular, the teeth tipped by the glands. Inflorescences axillary or false-terminal, racemose, sometimes contracted and thus appearing umbellate, axillary racemes usually present, 1-flowered and occurring in the leaf axils immediately below the false-terminal raceme, false-terminal racemes 2.2–5.5 cm long, (1–)3–9-flowered. Lower pedicels 2–11 mm long. Calyx 3–7 × 4–6 mm, campanulate, grayish green-stellate-pubescent; calyx teeth 5–7, unevenly distributed, to 2 mm long, narrowly deltoid or deltoid, usually contiguous, inner margin eglandular. Corolla white, 9–16 mm long, petals connate up to the calyx margin; corolla lobes 5(–10), imbricate in bud, 6–14 × 4–5 mm, overlapping, spreading, thin, broadly elliptic or obovate, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0.5–1.5 mm long; distinct portion of filament 4–6 mm long, of equal width throughout or sometimes narrowing distally, ventrally not auriculate, sparsely white-stellate-pubescent on the face, becoming glabrous distally, the hairs with arms to 0.15 mm long; anthers 4–4.5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely short-stellate-pubescent; style glabrous or pubescent at base only; stigma 0.3–0.7 mm wide. Capsule 8–11 × 7–11 mm, globose, 3-valve-dehiscent, the wall hard, stellate-canescent, coarsely and weakly longitudinally striate, not transversely wrinkled post-dehiscence. Seed coat glabrous.

Rare, occurring in southern Nayarit and adjacent portions of Jalisco, Mexico; 832–1700 m; *Quercus* or *Quercus-Pinus* forests; found in rocky places. Flowering: April–July; fruiting: September–December.

Additional specimens examined. MEXICO. **Jalisco:** S rim of the Barranca del Río Santiago, *Breedlove 61642* (CAS, MICH, NY); between km 17 and 18 on Hwy. Guadalajara–San Cristóbal de la Barranca, *Calzada et al. 17816* (MICH, RSA); Mpio. de Zapopan, Cerro del Diente, *Cházaro & Cházaro 6993* (TEX), *Guerrero et al. 322* (WIS); La Piedrera, *Nieves 50* (MEXU); Mpio. de Ahualulco, al NW de Chapulimita, 17 Sep. 1987, *Pérez s.n.* (IBUG); rocky hills near Guadalajara, *Pringle 3486* (GH); Sierra de San Esteban, *Pringle 4416* (F, MEXU, MICH, MO, NY, US, W), *Pringle 11012* (BH, F, GH, MICH, MO, NY, US); Mpio. de Zapopan, La Mesita de Sta. Lucía, *Ramírez 259* (IBUG); Guachinango, 20 Nov. 1982, *Robles s.n.* (IBUG); San Cristóbal de la Barranca, *Salazar 5* (IBUG); carretera a San Cristóbal de la Barranca, km 18, *Velázquez 13* (IBUG); Cerro del Tepopote, 20 km al W de Guadalajara, *Villarreal 4585* (IBUG, MICH). **Nayarit:** 8 km SE of San Leonel on Hwy. 15, *Breedlove & Almeda 45097* (CAS); km 192 on Hwy. 15 going NW from Tequila to Tepic, *Calzada et al. 17822* (MICH, RSA); 15 km NE of Santa Cruz de Guaybel, *Cházaro et al. 5485* (WIS); Ocotillo, *Gregg 955* (MO); between Ocotillo and Jazmines, ca. 25 mi. SE of Tepic, *McVaugh 12061* (MICH); 5 mi. SE of San Leonel, *McVaugh 13369* (MICH).

Styrax jaliscanus is the only deciduous *Styrax* species in western Mexico, so it is easily distinguishable from other sympatric members of the genus. This species was first collected near Ocotillo, Nayarit [28 May 1849, *Gregg s.n.*, date from McVaugh (1972)], but was left undescribed until Watson examined Pringle's 1889 collections. Perkins (1907) considered this species a variety of *S. officinalis* L., conferring upon the latter a highly disjunct distribution between southwestern Mexico, California, and the eastern Mediterranean region. *Styrax jaliscanus* does superficially resemble *S. officinalis* in its often orbicular and entire-margined leaves that are densely tomentose abaxially, and often contracted racemes. Upon closer inspection, however, the differences between these two species become apparent, including usually serrate versus always entire leaf margins, and prominent versus weak secondary and tertiary veins abaxially in *S. jaliscanus* and *S. officinalis*, respectively. The Californian representatives of *S. officinalis* have recently been treated as a species (*S. redivivus*) separate from *S. officinalis* in the Mediterranean region. Molecular phylogenetic analysis has confirmed that the relationship of *S. jaliscanus* to the lineage comprising deciduous *Styrax* taxa with entire leaf margins (*S. officinalis*, *S. platanifolius*, and *S. redivivus*) is distant (Fritsch, 1995, 1996a). According to the molecular data, *S. jaliscanus* is positioned in the same clade as the other deciduous, serrate-leaved species, i.e., the North American species *S. americanus*, *S. glabrescens*, and *S. grandifolius*, and many species of eastern Asia (Fritsch, 1995). Thus, I agree with Gonsoulin (1974) in maintaining species status for *S. jaliscanus*.

Gonsoulin (1974) reported *S. jaliscanus* to be a wide-ranging but sporadic species, occurring from extreme northern Baja California to Guerrero, Mexico. However, Gonsoulin made several errors concerning the range of this species: (1) he mistook two collections of *S. gentryi* (*Gentry 4420*, from Baja California Sur, and *Gentry 6244*, from Sinaloa) for *S. jaliscanus*; (2) he supposed that the Sierra de la Laguna is at the northern end of Baja California rather than the Cape Region of Baja California Sur; and (3) the Guerrero collection is cited in the revision as *Hinton 4583*; according to Hinton's collection list (Hinton & Rzedowski, 1972), this

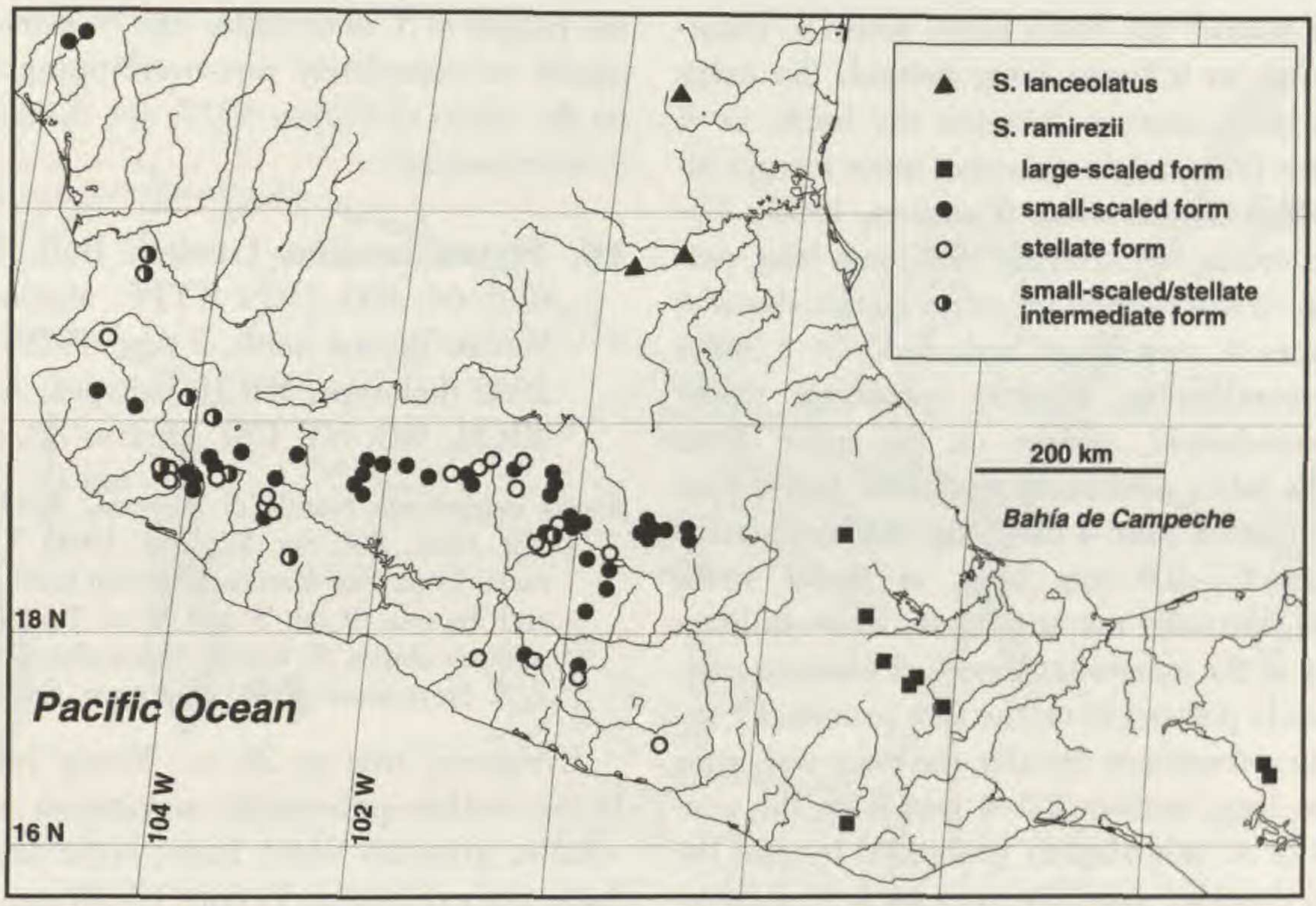


Figure 57. Distribution of *Styrax lanceolatus* and the forms of *S. ramirezii*.

number is actually *Apodanthera pringlei* S. Watson of the Cucurbitaceae, which could not possibly be mistaken for *Styrax*. There is no apparent explanation for Gonsoulin's erroneous citation of the Hinton collection—I do not know of any *S. jaliscanus* collections made by Hinton or anyone else from Guerrero.

Styrax jaliscanus, as circumscribed here, is a rare endemic to western Jalisco and Nayarit, Mexico. It was probably at one time more common in the hills surrounding Guadalajara, but habitat degradation resulting from overgrazing and fires has undoubtedly led to its decline there (pers. obs.). The risk of this species becoming extinct appears to be high. A detailed study entailing the documentation of all known populations, exploration within the range for yet undocumented populations, observation of life history parameters, examination of genetic variation patterns, and identification of threats to survival would help to identify the causes and possible mitigating measures that could be taken in order to protect this species. Toward this end, two populations of *S. jaliscanus* have been sampled for isozyme variation (Fritsch, 1996a).

I have selected the lectotype from two syntypes (*Pringle 2978* and *Pringle 3486*) cited in the protologue. I considered it best to designate *Pringle 2978* (GH) as the lectotype because (1) Gonsoulin (1974) cited *Pringle 2978* as the holotype and (2) Watson's original herbaria were US and GH (i.e., not A; Stafleu & Cowan, 1988).

The collection date of the type of *S. jaliscanus* is given as "1889" on labels but "1890" in the protologue.

9. Styrax lanceolatus P. W. Fritsch, nom. et stat. nov. Based on: *Styrax argenteus* var. *parvifolius* E. Carranza, Acta Bot. Mex. 23: 35. 1993. TYPE: Mexico. Querétaro: Mpio. de Arroyo Seco, ± 2 km al W de Agua Fría de los Fresnos, 23 Apr. 1992, *E. Carranza 4033* (holotype, IEB not seen; isotypes, CAS, ENCB not seen, MEXU not seen, MICH, XAL not seen). Figures 31, 57.

Evergreen tree to 6 m. Young twigs grayish green- or brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 7–12 mm long. Lamina chartaceous, 7.7–9.7 × 3.0–3.9 cm, lanceolate; apex narrowly acute to acuminate, secondary veins 8–9; base broadly cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with greenish white stellate hairs and scattered light orange-brown hairs on at least some leaves, the latter particularly prevalent near the veins, the whitish hairs covering on the secondary and tertiary veins, thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 1.7–5.0 cm long, 1–8-flowered. Lower pedicels 3–5 mm long. Calyx 3.5–4.5 × 4.5–6.0 mm, broadly cupuliform, grayish green-stellate-pubescent, with scattered orange-brown stellate hairs,

especially toward the base; calyx teeth 5, sometimes absent, to 0.3 mm long, deltoid, the calyx margin slightly concave between the teeth, or if teeth absent then margin truncate, inner margin often glandular. Corolla white (Carranza, 1993), 11–15(–17 according to Carranza, 1993) mm long, petals connate to just beyond the calyx margin distally; corolla lobes 5, valvate in bud, 8–11 × 1.5–2.5 mm, non-overlapping, slightly spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 4 mm long; distinct portion of filament 0.7–2.0 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, sparsely pubescent on the face proximally, increasing in pubescence distally, the hairs with arms to 0.5 mm long; anthers 3.5–4 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-tomentose; style and stigma not observed. Drupe 9–10(–11, according to Carranza, 1993) × 7–8(–9, according to Carranza, 1993) mm, ovoid-cylindric; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Rare in southern Tamaulipas and northern Querétaro, Mexico; 800–1500 m; *Quercus-Podocarpus* forests, wet forests; in Querétaro, found on hillsides and disturbed sites (Carranza, 1993). Flowering: October–January; fruiting: January–April (Carranza, 1993).

Uses. Occasionally made into posts in the construction of dwellings (Carranza, 1993).

Additional specimens examined. MEXICO. **Querétaro:** 2 km al W de Agua Fría de Los Fresnos, *Carranza 4465* (CAS). **Tamaulipas:** Rancho El Cielo, *Fairey T26M-79p-101490* (MICH, RSA); Gómez Farias region, *Johnston 7408* (TEX); Casa Piedra, ca. 2 km SW of Rancho del Cielo, *Johnston 12845* (TEX).

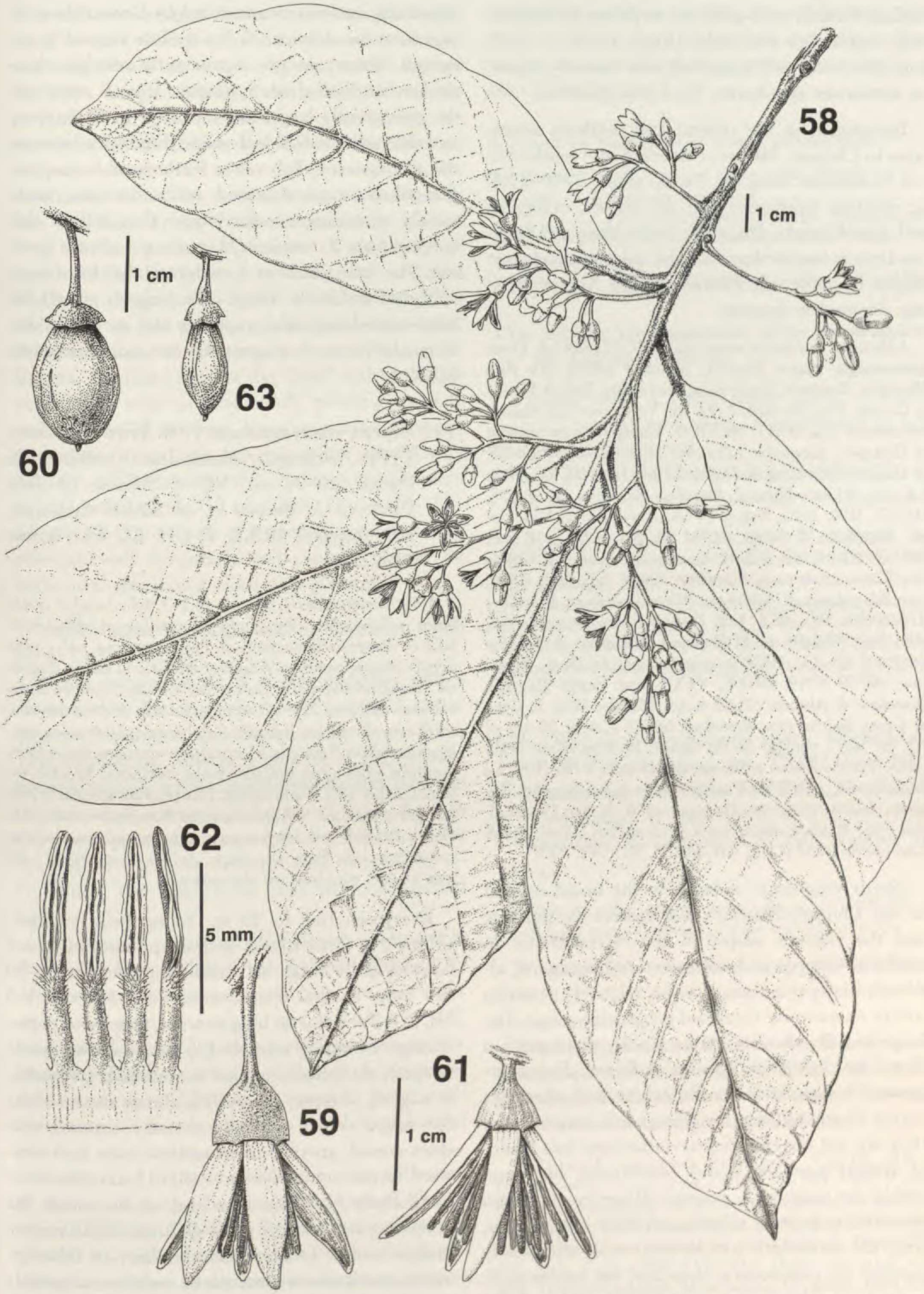
Styrax lanceolatus is a recently described rare endemic to southern Tamaulipas and western Querétaro, Mexico. It differs from sympatric species by its evergreen habit and stellate-pubescent calyx.

Carranza (1993) considered this species to be a variety of *Styrax argenteus* (var. *parvifolius*). However, in contrast to *S. argenteus* as circumscribed here, *S. lanceolatus* has non-tapered anther sacs, non-prolonged anther connectives, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. *Styrax warscewiczii* has many features in common with *S. lanceolatus,* but usually does not have the distinctive lanceolate leaves and always has a radiate-lepidote rather than a stellate-pubescent calyx. In addition, the ranges of *S. lanceolatus* and *S. warscewiczii* are nearly or completely non-overlapping (depending on the status of *Purpus 5317*; see discussion under *S. warscewiczii*).

10. Styrax magnus Lundell, Bull. Torrey Bot. Club 66: 600. 1939. TYPE: Mexico. Chiapas: Volcán Tacaná north, 2 Apr. 1939, *E. Matuda 2982* (holotype, MICH; isotypes, A, B, F, GH, MICH, MO, NY, US). Figures 32, 58–60.

Styrax vulcanicola Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 264. 1940. TYPE: Guatemala. Dept. San Marcos: between town of Tajumulco and Tecutla (9 mi. S and W of Tajumulco), northwestern slopes of Volcán Tajumulco, 27 Feb. 1940, *J. A. Steyermark 36801* (holotype, F (2 sheets)).

Evergreen tree to 26 m. Young twigs orange-brown-stellate-pubescent, sometimes mixed with smaller greenish white hairs; outer layer of older twigs not exfoliating. Petiole 17–30 mm long. Lamina chartaceous, 15.5–22.5 × 6.8–12 cm, usually obovate, sometimes broadly elliptic, secondary veins 10–20; apex abruptly short-acuminate to rounded; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute white stellate hairs and also variable amounts of larger white, rarely also orange-brown stellate and somewhat stiff hairs, the latter usually occurring on the veins, the minute hairs absent from the primary through tertiary veins thus the vein surface easily visible; margin entire. Inflorescences axillary or false-terminal, paniculate or rarely racemose, the racemes or panicle branches 1.5–4 cm long, 2–10-flowered. Lower pedicels 6–15 mm long. Calyx 3.5–5 × 4.5–6 mm, cupuliform or broadly cupuliform, grayish green-stellate-pubescent, occasionally with scattered larger orange-brown stellate hairs toward the base; calyx teeth 5, to 0.6 mm long, deltoid, the calyx margin truncate or slightly concave between the teeth, inner margin often glandular. Corolla white, (7–)11–12 mm long, petals connate 0–2 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, (7–)8–10 × (2–)3 mm, non-overlapping, spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 2 mm long; distinct portion of filament 1.0–1.2 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.5 mm long; anthers 5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely



Figures 58–63. 58–60. *Styrax magnus.* —58. Flowering branch. —59. Flower. 58, 59, *Breedlove 68742* (CAS). —60. Fruit, *Breedlove 46223* (CAS). 61–63. *Styrax radians.* —61. Flower, *McVaugh & Koelz 541* (MICH). —62. Four adjacent stamens. —63. Fruit. 62, 63, *Tenorio 15605* (MO).

stellate-hirsute; style glabrous or pubescent at base only; stigma 0.5 mm wide. Drupe 15–20 × 9–12 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Uncommon in the central and southern mountains in Chiapas, Mexico, extending into south-central Guatemala along the Pacific slope; 1700–2700 m; montane rainforests and dry forests, evergreen and mixed forests, *Magnolia-Podocarpus* and *Quercus-Drimys* forests; found on dry ridges, on volcanic slopes, in sandy soil. Flowering: May, August; fruiting: September–January.

Additional specimens examined. GUATEMALA. **Quezaltenango:** above Mujuliá, *Standley 85559* (F). **San Marcos:** Barranco Eminencia, above San Rafael Pie de la Cuesta, *Standley 68618* (F); Río Vega, near San Rafael, *Steyermark 36234* (F). MEXICO. **Chiapas:** near summit of Huitepec, *Alexander 1214* (MICH, NY); 45–50 km NE of Huixtla, *Breedlove & Thorne 31045* (DS, MEXU, MO); SW side of Cerro Mozotal, *Breedlove & Thorne 31106* (DS, MEXU, MO); Selva Negra, 10 km above Rayón Mezcalapa, *Breedlove & Smith 32394* (B, DS, DUKE, F, LL, MEXU, MICH, MO, NY, RSA); near the summit of Muk'ta vits (Cerro Huitepec), *Breedlove 39600* (DS, MO, RSA); near the summit of Muk'ta vits (Cerro Huitepec), *Breedlove 41446* (DS, MO, TEX, US); E slope Cerro Mozotal along road from Huixtla to El Porvenir, *Breedlove & Strother 46223* (CAS, LL, MEXU); near Colonia Ach'lum, *Breedlove 49750* (CAS, DUKE, TEX); near Paraje Banabil, *Breedlove & Almeda 57053* (CAS, MEXU, MO); E slope of Cerro Muk'ta vits, *Breedlove 68742* (CAS); 25 km al NE de San Cristóbal de las Casas, *Cabrera et al. 3805* (MO); Pueblo Nuevo a Simojovel, *Miranda 9170* (US); La Yerbabuena, al NW de Pueblo Nuevo Solistahuacán, *Palacios 161* (CAS); Cerro Huitepec al W de San Cristóbal, *Ton 7963* (CAS, F, MO); Santa Cruz en San Filipe, *Ton & Concepción 9734* (CAS, GH, MICH, MO, NY, TEX).

Styrax magnus is endemic to the broad summit of the Chiapas Plateau's wet eastern escarpment and the volcanic slopes of the Sierra Madre in southern Chiapas and southwestern Guatemala, although the species seems to be relatively common within its narrowly restricted geographic range. The large, usually obovate leaves readily distinguish it from other sympatric species of *Styrax*. *Styrax argenteus* occurs at lower elevations and often has leaves nearly as large as those of *S. magnus*, but they are not obovate. *Styrax incarnatus* has leaves of similar size and could conceivably be found within the range of *S. magnus*. However, its leaves are ovate or broadly elliptic and thick-chartaceous, with the secondary and tertiary veins completely covered by pubescence abaxially; the leaves of *S. magnus* are chartaceous, with the abaxial surfaces of the veins visible through the pubescence.

Gonsoulin (1974) subsumed *Styrax magnus* under his *S. argenteus* var. *hintonii*. I have maintained *S. magnus* as a species and assigned most of the remaining specimens annotated by Gonsoulin as *S. argenteus* var. *hintonii* to the stellate form of *S. ramirezii*. There are two consistently reliable characters that distinguish *S. magnus* from *S. ramirezii*: the consistently larger mature drupe of *S. magnus*, and the rather subtle leaf-shape difference between the two species. Two other features of *S. magnus* (branched, many-flowered inflorescences, more widely spreading corolla lobes) also delimit this species from *S. ramirezii*, but are not always present. The individuals of *S. ramirezii* that have been collected within the range of *S. magnus* are all the large-scaled form of the species and are easily distinguished from *S. magnus* by the radiate-lepidote calyx.

11. Styrax nicaraguensis P. W. Fritsch, sp. nov. TYPE: Nicaragua. Matagalpa: Cordillera de Darién, 28–31 mi. NE of Sebaco, 21 July 1962, *G. L. Webster et al. 12496* (holotype, MO; isotypes, DUKE, F, GH, LL, U). Figures 17–21, 47.

Arbor sempervirens; *lamina* 2.1–3.0plo longior quam latior, subtus pilis densis cinerascentibus-viridibus-stellatis et dispersis ferrugineis-stellatis instructa; *calyx* pilis densis cinerascentibus-viridibus-stellatis et saepe dispersis ferrugineis-stellatis instructus; *corolla* lobis in aestivatione valvatis, 2.5–4.0 mm latis, sub anthesi apertis, recurvis vel reflexis, linearibus-deltoideis; *filamenta* staminum partibus distinctis ad margines ventrales auriculatis, auriculis pilis albis-stellatis dense instructis, brachis pilorum usque ad 1.0 mm longis, illis pilorum apicem versus pro parte maxima ordinatis apicem floralibus versus; *antherae* 5.8–7.8 mm longae; *connectivum* antherae loculos contractos manifeste superans; *drupae* longiores 17–28 mm longae, ovoideae vel obovoideae.

Evergreen tree to 25 m. Young twigs orange-, yellow-, or gray-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 11–16 mm long. Lamina chartaceous, 8.5–14.5 × 3.4–5 cm, 2.1–3.0 times as long as wide, elliptic or ovate-oblong, secondary veins 8–11; apex narrowly acute to acuminate; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially densely covered with short-armed, grayish green stellate hairs and scattered larger orange-brown stellate hairs, the latter particularly prevalent near and on the veins, the secondary and tertiary veins glabrous or pubescent; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, racemes or panicle branches 2.3–7 cm long, 2–10-flowered. Lower pedicels 5–9 mm long. Calyx 3.5–5 × 4–6 mm, cupuliform, grayish green-stellate-pubescent, often with larger orange-brown stellate hairs especially toward the base; calyx teeth 5, to 0.3 mm long,

deltoid, calyx margin truncate between the teeth, inner margin often glandular. Corolla white, 13–15 mm long, petals not or only slightly connate beyond the calyx margin distally; corolla lobes 5, valvate in bud, 9–11 × 2.5–4 mm, non-overlapping, recurved or reflexed, thin, linear-deltoid, vesture on the outer distal third of the lobes consisting predominantly of radiate scales, best seen in the mature bud stage. Free portion of stamen tube 1.5 mm long; distinct portion of filament 2 mm long, of equal width throughout, ventrally with auricles bearing a dense mass of stiff white stellate hairs with arms to 1.0 mm long, also pubescent below the auricles and at the sinus between adjacent filaments, the hairs nearest the distal end of the filament with arms predominantly pointing upward; anthers 5.8–7.8 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3 mm wide. Drupe (15–)17–28 × (10–)11–14(–15 if 2-seeded) mm, ovoid or obovoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Northwestern Nicaragua and northwestern Costa Rica; 1100–1550 m.

Styrax nicaraguensis is a rare endemic with a disjunct distribution in the cloud forests of northwestern Nicaragua and northwestern Costa Rica. This disjunction reflects a paucity of high mountainous regions with cloud forest habitat between the two areas where it is known to exist. Enough time has apparently elapsed during separation for the disjuncts to have differentiated morphologically; hence, two subspecies have been designated here.

This species is probably the closest relative of *S. argenteus*, from which it can be distinguished by the presence of orange-brown hairs on the calyx and lower laminar surface, and the shorter stiff, long-armed, upward-pointing stellate hairs on the stamen filaments ventrally. Although *S. argenteus* does reach up to 1500 m elevation in many parts of its range, it does not occur in cloud forest habitat where *S. nicaraguensis* occurs.

Gonsoulin (1974) identified the only collection of this species seen by him at the time of his revision (*Williams 23955*) as *Styrax argenteus* var. *argenteus* (the annotation label on one of the duplicates states "close to var. *ramirezii*"). Because these specimens are either sterile or possess inflorescences with only pedicels and calyces, it is understandable that Gonsoulin overlooked the subtle vegetative differences between this species and the others in Central America. However, the collection Gonsoulin saw does present unusual features with respect to the rest of the material available to him, and it is surprising that no mention was made of this in his revision.

KEY TO THE SUBSPECIES OF *STYRAX NICARAGUENSIS*

1a. Fruiting calyx ± rotate; drupe ovoid, deeply rugose on herbarium specimens ..... 11a. *S. nicaraguensis* subsp. *nicaraguensis*

1b. Fruiting calyx cupuliform; drupe obovoid, shallowly rugose on herbarium specimens ..... 11b. *S. nicaraguensis* subsp. *ellipsoidalis*

11a. Styrax nicaraguensis subsp. **nicaraguensis**. Figures 17–20, 47.

Fruiting calyx ± rotate; drupe 17–21 × 13–14 (–15 if 2-seeded) mm, ovoid, deeply rugose on herbarium specimens.

Rare in northwestern Nicaragua; 1300–1550 m; cloud forests. Flowering: June–July; fruiting: June.

Additional specimens examined. NICARAGUA. **Estelí:** Laguna de Miraflores, *Atwood A316* (MEXU, MO, NY). **Jinotega:** Laguna de Miraflores, 8 June 1975, *Atwood s.n.* (MO); km 146 carretera Matagalpa–Jinotega, *Moreno 16366* (MO); along Hwy. 3, ca. 1 km NW of La Fundadora entrance, *Stevens & Henrich 20401* (MO). **Matagalpa:** Sta. María de Ostuma, *Williams et al. 23955* (F, NY, US, W).

11b. Styrax nicaraguensis subsp. **ellipsoidalis** P. W. Fritsch, subsp. nov. TYPE: Costa Rica. Puntarenas: Cordillera de Tilarán, Monteverde Comunidad, 6 June 1977, *V. J. Dryer 1420* (holotype, F; isotypes, CR, MO). Figures 21, 47.

Calyx fructifer cupuliformis; *drupa* (15–)19–28 × (10–)11–13 mm, obovoidea, rugosa tenuiter in sicco.

Fruiting calyx cupuliform; drupe (15–)19–28 × (10–)11–13 mm, obovoid, shallowly rugose on herbarium specimens.

Northwestern Costa Rica in the Cordillera de Guanacaste and the Cordillera Tilarán on the Pacific slope; 1100–1500 m; forest edges. Flowering: July, November; fruiting: April–June.

Additional specimens examined. COSTA RICA. **Guanacaste:** Cerro Cacao, *Chávez 540* (CR, INB); Parque Nacional Guanacaste Estación Mengo, Cerro Cacao *II INBio 164* (CR, MO). **Puntarenas:** Río Guacimal, *Bello 932* (CR, INB); Monteverde, *Dryer 1420* (CR, F), *Dryer 1575* (CR, MO), *Fuentes 192* (INB, MO), *Haber 230* (AAU, CR, MO); in Mata's pasture, Monteverde, *Hartshorn 1894* (CR, F, MO).

The *II INBio 164* collection has smaller leaves and fruit (15 × 10 mm) than other collections, but its other features leave no doubt as to its identity.

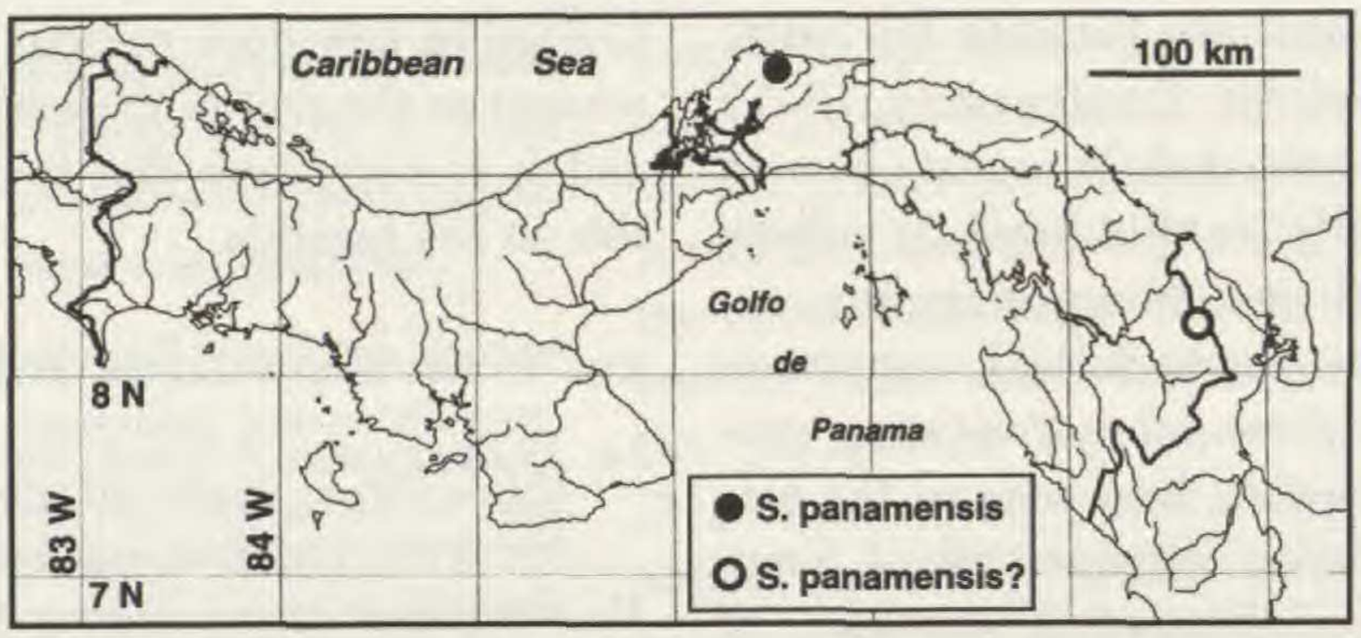


Figure 64. Distribution of *Styrax panamensis*; see text for explanation of dubious record.

12. Styrax panamensis Standl., Contr. U.S. Natl. Herb. 18: 121. 1916. TYPE: Panama. Colón: Loma de la Gloria, near Fató (Nombre de Dios), July and Aug. 1911, *H. Pittier 4242* (holotype, US-679343; isotypes, GH, NY, US). Figures 11, 64.

Evergreen tree to 10 m. Young twigs golden brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 6–16 mm long. Lamina chartaceous, 11.5–12 × 8–8.2 cm, 1.5 times as long as wide, broadly obovate, secondary veins 6–8; base cuneate, symmetric or slightly oblique; apex acuminate or emarginate through abortive tip development; adaxially glabrous except along the major veins; abaxially covered with minute white stellate hairs and scattered larger, grayish white, somewhat stiff stellate hairs, the latter occurring most frequently on the veins, the minute hairs absent from the primary through tertiary veins thus the vein surface easily visible; margin entire. Specimens in bud only. Inflorescences racemose, axillary or false-terminal, 3–4.5 cm long. Lower pedicels 5 mm long. Calyx 6 × 5 mm, narrowly cupuliform, uniformly golden brown-stellate-pubescent; calyx teeth 5, minute, deltoid, the calyx margin truncate or slightly concave between the teeth, inner margin apparently eglandular. Corolla in bud 11 mm long; corolla lobes 5, valvate in bud, 7–8 × 2 mm, linear-deltoid, vesture of the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0.8 mm long; distinct portion of filament 0.8 mm long, slightly flexuous, of equal width throughout, ventrally not auriculate, densely covered across the face with tawny, undulating to somewhat stiff stellate hairs with arms to 0.8 mm long, the hairs nearest the distal end of the filament with arms predominantly pointing upward; anthers 5 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary short-stellate-pubescent; style glabrous. Fruit unknown.

Endemic to western Panama; 10–104 m; forests. Flowering (in bud only): July, August.

Styrax panamensis is known with certainty only from the type collection. Its occurrence in low-elevation tropical forest habitat is unusual with respect to the other *Styrax* species treated in this revision. Fruiting specimens from 1550 to 1650 m elevation in the Serranía del Darién [*Gentry & Mori 13797* and *14073* (MO)] might belong to this species, but they have smaller leaves with long-acuminate apices. A fruiting specimen from 150 m elevation in Mpio. de Hidalgotitlán, Veracruz, Mexico (17°15′45″N, 94°29′30″W, *Wendt 3576*), also may be this species. More material, particularly good flowering and fruiting material of plants from near Pittier's collection site, as well as material at anthesis from the Darién region and the locality at Veracruz will be required to better understand *Styrax* in these areas.

Although only flower buds are available on the type, careful analysis of internal floral morphology suggests that *S. panamensis* is allied to other lowland South American species (e.g., *S. guianensis*) that lack auricles but possess a dense mass of hair with relatively long arms (> 0.7 mm) on the ventral side of the stamen filaments.

Perkins apparently did not see the Pittier collection. Gonsoulin (1974) annotated it as *Styrax argenteus* var. *ramirezii* (= *S. argenteus* var. *micranthus*; see comments under *S. ramirezii*).

13. Styrax peruvianus Zahlbr., Ann. K. K. Naturhist. Hofmus. 7: 4. 1892. TYPE: Peru. Cajamarca: Tambillo, *Jelski 16* (holotype, W; isotypes, B destroyed, photo in F, GH, MICH, MO, NY). Figures 13, 36–39, 47.

Evergreen tree to 10 m. Young twigs lepidote, the scales brown mixed with olive-green; outer layer of older twigs not exfoliating. Petiole (7–)10–15 mm long. Lamina thick-chartaceous, 6.5–12 × 2.2–5 cm, 2.0–3.1 times as long as wide, lance-

elliptic or oblanceolate, secondary veins 7–9; apex abruptly short-acuminate to rarely acuminate; base cuneate to slightly attenuate, symmetric or slightly oblique; adaxially glabrous or sparsely lepidote; abaxially covered (surface and veins) with olive-green peltate or lacerate-margined scales, and more scattered orange-brown scales; margin entire. Inflorescences racemose, axillary or false-terminal, 3.5–8.5 cm long, 3–9-flowered. Lower pedicels 8–14 mm long. Calyx 3–3.5 × 4.5 mm, cupuliform, olive-green lepidote with scattered light orange-brown scales, scales 0.27–0.44 mm diam., peltate or lacerate-margined; calyx teeth 5, to 0.5 mm long, deltoid; calyx margin slightly concave or rarely truncate between the teeth, inner margin often glandular. Corolla pink, 10–16 mm long, petals connate 1–3 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 7–10 × 1.8–3.2 mm, non-overlapping, spreading to recurved, linear-deltoid, thickened, vesture on the outer distal third of the lobes consisting of peltate or lacerate-margined scales. Free portion of stamen tube 1–1.7 mm long; distinct portion of filament 1.5–2.0 mm long, of equal width throughout; ventrally with prominent auricles bearing radiate scales or stellate hairs with arms 0.1–0.3 mm long, glabrous elsewhere; anthers 4–5.5 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary lepidote; style glabrous or pubescent at base only; stigma 0.3–0.4 mm wide. Drupe 11–20 × 5–10 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Northwestern Costa Rica to western Panama; also Colombia, Ecuador, and Peru; 1600–2100 m; lower montane rainforests, mixed forests; found on windswept ridges and in forest understory. Flowering: July–August; fruiting: January, June, October.

Additional specimens examined. COSTA RICA. **Alajuela:** Monteverde Reserve, El Valle Trail near continental divide, *Haber ex Bello 3173* (MO). **Guanacaste:** Parque Nacional Guanacaste, Fila Orosilito, *I INBio 16* (CR, F, MO). **Puntarenas:** Monteverde Reserve, Senderos Chomogo and Pantanoso, *Haber & Zuchowski 9318* (CR, INB). PANAMA. **Chiriquí:** Cerro Colorado, along mining road 31.6 km beyond bridge over Río San Félix, *Croat 37190* (MO, NY); Cerro Pate Macho, *de Nevers & McPherson 6848* (CAS, MO).

Styrax peruvianus is easily distinguished from other sympatric species by the peltate or lacerate-margined scales on the leaves, branches, and inflorescences. The only other species in the region with this feature is *S. conterminus*, which has narrowly elliptic leaves, non-auriculate stamen filaments, and non-tapered anther sacs.

This species has been only rarely collected throughout its range. The description given here is based on the specimens cited above and the following: *L. Ellemann 66559* (LOJA, QCA; Ecuador), *G. Lozano C. 2537* (COL; Colombia), *R. Sandino-Pardo 11* (COL; Colombia), and *B. Wallnöfer 18-1588* (W; Peru). *Styrax peruvianus* is considered to belong to a lineage comprising several species in South America with peltate scales, stamen filaments with auricles and/or dense pubescence with long-armed hairs (> 0.8 mm) ventrally, and prolonged anther connectives, including *S. cordatus* and *S. leprosus*.

14. Styrax platanifolius Engelm. ex Torr., Smithsonian Contr. Bot. 6: 4. 1854 ["*S. platinifolium*"]. TYPE: U.S.A. Texas: Comal Co., near New Braunfels, 1851, *Lindheimer s.n.*, (holotype, MO; isotype, GH). Figures 55, 56, 65, 66.

Deciduous shrub multi-stemmed from the base, to 3 m. Young twigs glabrous to densely white-stellate-pubescent, sometimes somewhat glaucous, often toward the base with scattered orange-brown or dark brown stalked stellate hairs; outer distal layer of older twigs often exfoliating into long strips. Petiole 6–20 mm long. Lowest leaf pair on each twig usually alternate, sometimes subopposite. Lamina chartaceous, 4.5–9.0(–12) × 4.2–9(–11.5) cm, depressed-orbicular or very broadly ovate, sometimes slightly conduplicate, as evidenced by longitudinally folded laminae on herbarium specimens, secondary veins 5–6; apex rounded or obtuse, rarely acute, sometimes broadly cuspidate; at least some leaf bases on each leaf cordate or truncate, others rounded, usually slightly attenuate, symmetric or slightly oblique; adaxially glabrous or pubescent; abaxially glabrous or thickly covered with white stellate hairs, with scattered, orange-brown or dark brown stalked stellate hairs especially prevalent on veins and the lowest pair of leaves on each shoot, the stellate portion often deciduous from the base, the secondary and tertiary veins evident but not prominent; margin usually eglandular, either entire or apically with 2–several lobes or coarse teeth. Inflorescences false-terminal, sometimes contracted and thus appearing umbellate, 2–5 cm long, 1–7-flowered. Lower pedicels 4–9 mm long, becoming wider from base to apex, 1.3–2.3 times as long as the calyx. Calyx 3–5(–6) × 4.5–5.5 mm, campanulate, glabrous or densely white-stellate-pubescent, margin and/or teeth at least sparsely glandular; calyx teeth 0–7, irregularly distributed, to 1 mm long, narrow-deltoid or linear, the calyx margin truncate between the teeth. Corolla white, 12–21 mm long, petals con-

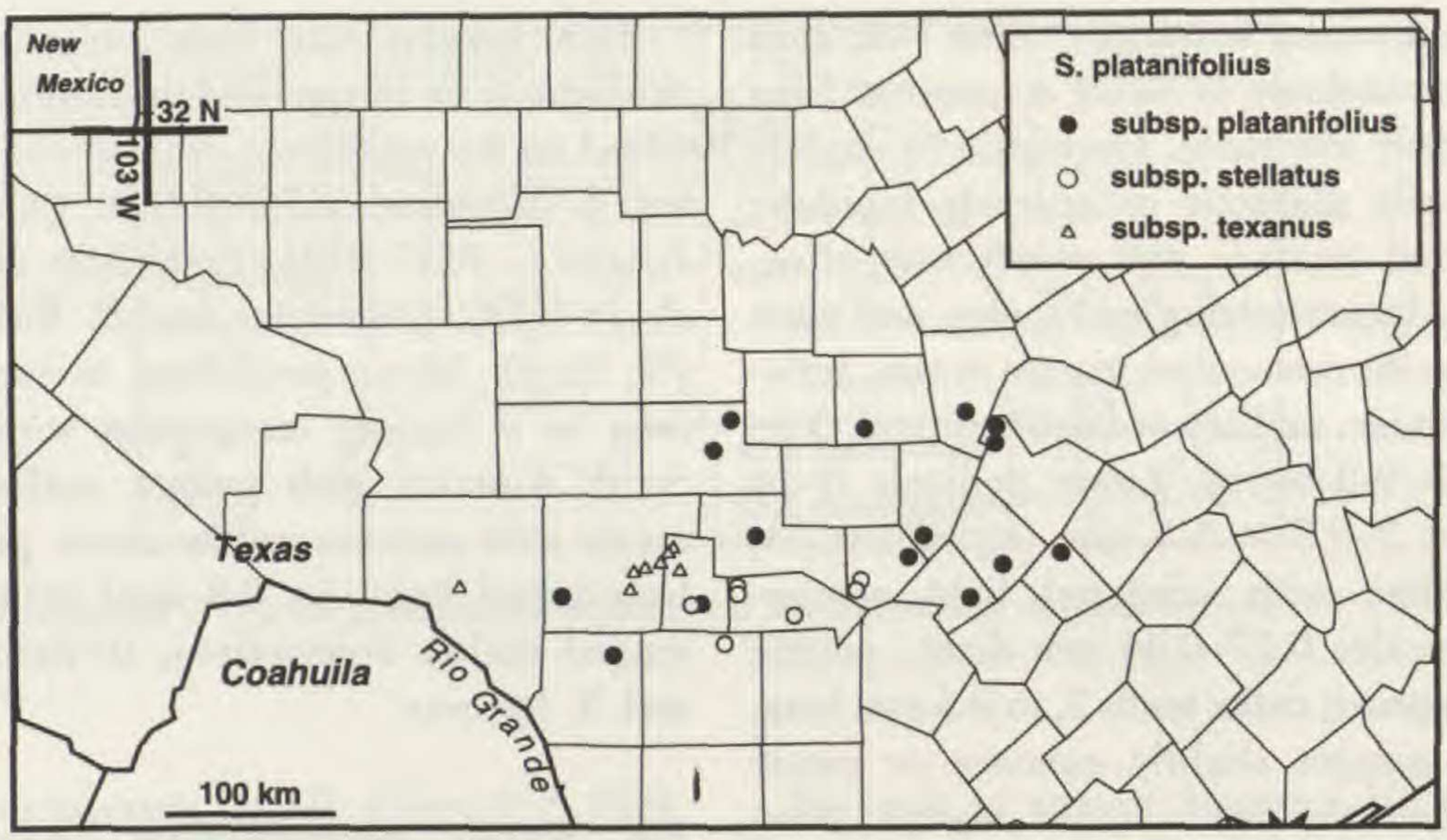


Figure 65. Distribution of *Styrax platanifolius* subsp. *platanifolius*, *S. platanifolius* subsp. *stellatus*, and *S. platanifolius* subsp. *texanus*.

nate up to the calyx margin distally; corolla lobes 5(6), imbricate in bud, 11–18 × 3–7 mm, overlapping, spreading, thin, elliptic, vesture on the outer distal third consisting of stellate hairs. Free portion of the stamen tube 1–6 mm long; distinct portion of filament 2–9 mm long, of equal width throughout, ventrally not auriculate and sparsely white-stellate-pubescent, becoming glabrous toward the distal end of the filament, the hairs with arms to 0.15 mm long; anthers 3–5.5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely short-stellate-pubescent; style pubescent at base only to nearly throughout; stigma 0.3–0.7 mm wide. Capsule 7–10 × 7–11 mm (broader when 2–3-seeded), globose, 3-valve-dehiscent, the wall hard, stellate-canescent, smooth but usually transversely wrinkled post-dehiscence. Seeds 6–9.5 mm long; seed coat glabrous.

West-central Texas on the Edwards Plateau escarpment and in the Davis Mountains, to Coahuila and Tamaulipas, Mexico, where it exists along the



Figure 66. Distribution of *Styrax platanifolius* subsp. *mollis* and *S. platanifolius* subsp. *youngiae*.

Table 1. Characters differentiating *Styrax platanifolius* from *S. redivivus* (modified from Fritsch, 1996b).

Character	*S. platanifolius*	*S. redivivus*
larger undehisced capsules	7–10 mm long	11–15 mm long
larger seeds	6–9.5 mm long	9.5–12 mm long
mature capsule pubescence	canescent	tawny or fulvous
pedicel/calyx length (ratio)	1.3–2.3	0.5–1.4
calyx	3–5 (–6) × 4.5–5.5 mm	4–7 × 5–7 mm
leaf margins	often coarsely lobed or irregularly undulate	never lobed

northeastern escarpment of the Sierra Madre Oriental, and the Chihuahuan desert mountains; 200–2000 m; dry wooded bottomlands, rocky stream banks and ledges, wooded canyons, izotal vegetation; found on limestone, and according to Cory (1943), igneous soil in the Davis Mountains.

After publication of *S. platanifolius* (Torrey, 1853), no new *Styrax* taxa from Texas were published until Cory (1943) described two new species (*S. texanus* and *S. youngiae*) and one new variety (*S. platanifolius* var. *stellatus*) from the Edwards Plateau and the Davis Mountains. Gonsoulin (1974) agreed completely with Cory's assessment of the genus in Texas and incorporated material collected in northern Coahuila and not seen by Cory into *S. youngiae.*

Data from morphology (Fritsch, 1996b), isozymes (Fritsch, 1996a), and DNA sequences (Fritsch, 1995) strongly suggest that these taxa are more closely related to each other than to other taxa of *Styrax.* However, in my opinion the morphological variation within and among these taxa warrants the recognition of only one species of *Styrax* from Texas. Cory (1943) and Gonsoulin (1974) presented a summary table of differences among *S. platanifolius, S. texanus,* and *S. youngiae.* Most of the characters in this summary (i.e., upper leaf surface color, calyx color, presence of calyx glands, vein reticulation on lower leaf surface) are not taxonomically reliable upon close inspection of the collections. The remainder involve differences in the quantity of pubescence on the vegetative parts, pedicels, and calyces that I consider to be taxonomically inconsequential within many other species of *Styrax,* such as *S. glabrescens, S. grandifolius,* and *S. redivivus.* To place this variation in perspective, there are reliable characters separating members of this group from the closely related species *S. redivivus,* endemic to California (Fritsch, 1995, 1996b; Table 1).

Additional evidence for the recognition of only a single species of *Styrax* from Texas comes from isozyme analysis (Fritsch, 1996a). Pairwise genetic identities (*I*) estimated from isozyme allelic variation between populations of *S. platanifolius* subspp. *texanus* and *stellatus* range from 0.986 to 0.991, which is within the 0.90–1.00 range expected among infraspecific taxa (Crawford, 1983). In contrast, pairwise estimates of *I* between populations of *S. redivivus* from California and all taxa from Texas sampled is 0.446, well below the reported average among congeneric species (0.67; Gottlieb, 1977; Crawford, 1983, 1989). Because only four populations within *S. platanifolius* were sampled, it would be desirable to obtain more isozyme data from additional populations, especially for subspecies *platanifolius, youngiae,* and *mollis.* In this regard, one individual sampled of subspecies *mollis* (= *S. youngiae* in Fritsch, 1996a) exhibited several alleles not shared by any individuals of subspecies *stellatus* or *texanus* (= "*S. platanifolius stellatus*" and "*S. texanus*" in Fritsch, 1996a, respectively).

Although the variation present is not considered sufficient to confer species status to *Stryrax texanus* and *S. youngiae,* an argument can be made for retaining these taxa as subspecies within *S. platanifolius.* Variation in pubescence quantity in other New World species of *Styrax* is either not at all or only poorly associated with geography, ecology, or life history (*S. glabrescens, S. grandifolius*), or at most is distributed along latitudinal clines (*S. americanus, S. redivivus*), and I do not recognize infraspecific taxa within these species. In contrast, trichome morphology or abundance within *S. platanifolius* is distinctly regional and facilitates the delimitation of nearly or completely allopatric taxa. Therefore, I have recognized five subspecies within *S. platanifolius* based on minor but distinctive differences. Trichome characters are those most reliable for the delimitation of these subspecies; characters of secondary importance include leaf form, calyx gland density, and surface features of the stem.

Gonsoulin (1974) incorrectly attributed the description of *S. platanifolius* to "Boston J. Nat. Hist. 6: 146–147, 1854." The article to which I presume he was referring (Gray, 1850) is the second of a three-part account of F. Lindheimer's collections in

western Texas. Because it covers the collections from the years 1845–1848, this article would not be expected to list the 1851 *S. platanifolius* collection in any case. The other two parts to the series (Engelmann & Gray, 1845; Blankinship, 1907) also do not cite the collection.

KEY TO THE SUBSPECIES OF *STYRAX PLATANIFOLIUS*

1a. Abaxial laminar surface glabrous or visible through the pubescence.
  2a. Leaves, pedicels, and calyces without white stellate hairs ..... 14a. *S. platanifolius* subsp. *platanifolius*
  2b. Leaves, pedicels, and calyces with white stellate hairs.
    3a. Longest arms of each stellate hair on the abaxial laminar surface typically about 0.8 mm long, often exceeding 1 mm; laminar surface soft to the touch; calyx teeth to 0.3 mm long, the calyx margin sparsely glandular ..... 14b. *S. platanifolius* subsp. *mollis*
    3b. Longest arms of each stellate hair on the abaxial laminar surface typically about 0.4 mm long, rarely if ever reaching 1 mm; laminar surface somewhat rough to the touch; calyx teeth to 1 mm long, the teeth and calyx margin densely glandular 14c. *S. platanifolius* subsp. *stellatus*
1b. Abaxial laminar surface completely covered and obscured by the pubescence.
  4a. Young twigs faintly glaucous; abaxial laminar surface, pedicels, and calyces with a thin and even layer of white stellate pubescence; adaxial laminar surface glabrous; style pubescent from base to ca. 15–35% of the total length ..... 14d. *S. platanifolius* subsp. *texanus*
  4b. Young twigs stellate-pubescent; abaxial laminar surface, pedicels, and calyces with a thick layer of white stellate pubescence; adaxial laminar surface stellate-pubescent; style pubescent from base to ca. 60–80% of the total length ..... 14e. *S. platanifolius* subsp. *youngiae*

14a. Styrax platanifolius subsp. **platanifolius.** Figure 65.

Young twigs glabrous except for scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina glabrous on both sides except for scattered orange-brown or dark brown stalked stellate hairs abaxially on some leaves, margin often irregularly undulate, weakly 3-lobed, or coarsely toothed, less often entire. Pedicel and calyx glabrous. At least some calyx teeth to 1 mm long, the teeth and calyx margin densely glandular. Style pubescent from base to 15–35% of the total length.

Rare, occurring in west-central Texas on the Edwards Plateau escarpment; 200–700 m; dry wooded bottomlands, rocky banks and ledges. Flowering: April–May; fruiting: July–September.

Common name. Sycamore-leaf snow-bell (Gonsoulin, 1974).

Additional specimens examined. UNITED STATES. **Texas:** County unknown: San Marcos and vicinity, summer 1897, *Stanfield s.n.* (NY); Bull Cr., Mr. J. Beard's place, 14 Apr. 1915, *Young s.n.* (TEX). Blanco Co.: Little Blanco River near intersection of Hwy. 281 and 473, *Dorr & Nixon 1910* (NY); bluff overlooking Little Blanco River, S of Twin Sisters, *Gonsoulin 1289* (NY); Little Blanco River and Hwy. 66–281, 24 Aug. 1947, *Parks s.n.* (LL); intersection of Hwy. 281 and 473 on N bank of Little Blanco River, 29 Apr. 1972, *Welborn & Sanstrup s.n.* (TEX). Burnet Co.: 3 mi. N of Smithwick, *Henry 6557* (GH); 12 mi. WSW of Bertram, 16 June 1950, *Tharp s.n.* (TEX). Caldwell Co.: ca. 4.5 mi. W of Delhi on TX 713, *Gonsoulin 1287* (NY). Edwards Co.: ravine near W Nueces River, ca. 19 mi. SW of Rocksprings, *Gonsoulin 1306* (NY). Hays Co.: near Lake Travis, 9.3 mi. WNW of Cedar Creek, *Gonsoulin 1288* (NY). Kendall Co.: near Edge Falls along Curry Creek, *Correll 29152* (GH, LL); below Edge Falls, ca. 5 mi. S of Kendalia, *Correll & Smith 29572* (GH, LL); Edge Falls, *Correll & Correll 37024* (LL). Kerr Co.: near Guadalupe River, ca. 4 mi. W of Hunt, *Gonsoulin 1305* (NY). Kimble Co.: one half mi. E of Junction near Hwy. 290, 18 May 1960, *Coleman s.n.* (TEX); Junction, *Palmer 10907* (A); Big Saline Creek, *Reverchon 1551* (GH). Kinney Co.: on banks of Nueces River, *Gonsoulin 1307* (NY). Llano Co.: Enchanted Mountain, 26 June 1932, *C. E. A. s.n.* (TEX); Enchanted Rock, *Jermy s.n.* (NY), *Jermy 105* (MO), 12 June 1930, *Whitehouse s.n.* (GH, NY), 25 Apr. 1931, *Whitehouse s.n.* (TEX), 16 Aug. 1931, *Whitehouse s.n.* (TEX). Real Co.: ca. 4.5 mi. E of Leaky on TX 337, *Gonsoulin 1308* (NY). Travis Co.: cultivated at 1405 Rabb Rd. in Austin, *Correll & Correll 37003* (LL); Austin, Apr. 1913, *Huppetz s.n.* (TEX); Travis Peak, Austin, 3 May 1930, *Prowse s.n.* (TEX), 3 May 1930, *Whitehouse s.n.* (GH); near Austin, *Wright s.n.* (GH).

This is the most widespread of the three subspecies of *Styrax platanifolius* endemic to Texas, but it is extremely rare throughout its range. Populations apparently were larger and more common in the early 1900s, but the subspecies has since declined dramatically (Cory, 1943; J. Poole, Texas Parks and Wildlife Department, Austin, Texas, pers. comm.; pers. obs.). Many populations have been extirpated, and those that remain often consist of only a single individual or a few plants. Documentation and monitoring of remaining populations, assessment of genetic variation among all remaining individuals, and management plans are desperately needed to ensure the survival of members of this subspecies.

14b. Styrax platanifolius subsp. **mollis** P. W. Fritsch, subsp. nov. TYPE: Mexico. Coahuila: Mpio. de Muzquiz, Rancho Agua Dulci, E slope of the Sierra de San Manuel, 28 June 1936, *F. L. Wynd & C. H. Mueller 340* (holotype, MO; isotypes, A, MICH, NY). Figure 66.

Lamina alba-stellata-pubescens utrinque, subtus ad tactum mollis, brachis longissimis pilorum stellatorum typice 0.8 mm longis, saepe excedentibus 1 mm longis, pagina abaxiali visibili infra tomento; *pedicelli* albi-stellati-pubescentes; *calyx* alba-stellata-pubescens, margine inferme glandifero, dentibus usque ad 0.3 mm longis.

Young twigs densely white-stellate-pubescent in addition to scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above with scattered stellate pubescence, the hairs most often simple, sometimes stellate and then to about 4-armed, below moderately densely white-stellate-villous in addition to scattered orange-brown or dark brown stalked stellate hairs on some leaves, soft to the touch, the surface visible through the pubescence, the longest arms of each stellate hair typically about 0.8 mm and often exceeding 1 mm long, margin often usually entire, less often weakly undulate. Pedicel and calyx with white stellate hairs of variable length. Calyx teeth to 0.3 mm long, the calyx margin sparsely glandular. Style pubescent from base to 30–75% of the total length.

Rare, Coahuila and Tamaulipas, Mexico, along the eastern escarpment of the northern extension of the Sierra Madre Oriental and Chihuahuan desert mountains; 1200–1400 m; wooded canyons. Flowering: April.

Additional specimens examined. MEXICO. **Nuevo León:** Monterrey, Chipinque, *Peterson 1243* (TEX); Monterrey, La Silla Trail, *Smith M149* (TEX).

I have also seen individuals of this subspecies cultivated at the Berkeley Botanic Garden, Berkeley, California (accession number 91.1305), originally collected by J. Fairey (Yucca Do Nursery, Waller, Texas) from Purificación, Tamaulipas, Mexico.

Styrax platanifolius subsp. *mollis* is a rare endemic to Coahuila and Tamaulipas, Mexico. It is the southernmost of the five subspecies recognized in *S. platanifolius,* having no apparent range overlap with the nearest subspecies to the north (subsp. *youngiae*), from which it is distinguished by the soft pubescence that does not completely cover the lower laminar surface. The distinctness of this subspecies from subspecies *youngiae* is highlighted by Gonsoulin's (1974) ambiguity regarding its identification. He cited the only specimen available to him of this subspecies (*Wynd & Mueller 340*) as *S. youngiae,* but annotated it as *S. platanifolius* var. *stellatus,* probably because subspecies *stellatus* resembles subspecies *mollis* more closely than does subspecies *youngiae.*

14c. Styrax platanifolius subsp. **stellatus** (Cory) P. W. Fritsch, comb. et stat. nov. Basionym: *Styrax platanifolius* var. *stellatus* Cory, Madroño 7: 111. 1943 ["*S. platanifolius* var. *stellata*"]. TYPE: U.S.A. Texas: Bandera Co., Sabinal Canyon, 16 June 1940, *V. L. Cory 34765* (holotype, A; isotype, NY). Figure 65.

Young twigs sparsely white-stellate-pubescent in addition to scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above with scattered stellate pubescence, the hairs with 6–14 arms, below with scattered white stellate pubescence in addition to scattered orange-brown or dark brown stalked stellate hairs on some leaves, somewhat rough to the touch, the surface visible through the pubescence, the longest arms of each stellate hair typically about 0.4 mm long, rarely if ever reaching 1 mm, margin often irregularly undulate, weakly 3-lobed, or coarsely toothed, less often entire. Pedicel and calyx with white stellate hairs of variable length. At least some calyx teeth to 1 mm long, the teeth and calyx margin densely glandular. Style pubescent from base to 50–70% of the total length.

Rare in west-central Texas on the Edwards Plateau escarpment; 500–700 m; dry wooded bottomlands, rocky banks and ledges. Flowering: April–May; fruiting: July–September.

Common name. Hairy sycamore-leaf snow-bell (Gonsoulin, 1974).

Additional specimens examined. UNITED STATES. **Texas:** Bandera Co.: 1 mi. N of Vanderpool, 15 June 1940, *Cory s.n.* (GH); Sabinal Canyon, 6.5 mi. N of Vanderpool, *Cory 34763* (TEX); Can Creek, 7 mi. N of Vanderpool, *Cory 49453* (LL), *Cory 49454* (A); Sabinal River, 7.5 mi. N of Vanderpool, *Henry 6560* (GH); steep ravine 9 mi. W of Boerne, *Johnson & Webster 599* (TEX); Upper Seco Creek, *Palmer 10237* (GH); Vanderpool, *Palmer 11528* (GH, MO, NY, POM); 2 mi. N of Vanderpool, *Parks 1009* (A); Vanderpool, *Parks 1942* (TEX), *Parks 40988* (A); Lost Maples State National Area, along the Sabinal River, *Poole & Watson 1205* (LL); Sabinal Canyon State Park, *Riskind & Snyder 1682* (LL, MO); Lost Maples State Natural Area, Hales Hollow, *Smith 517* (LL, NY); Lost Maples State National Area, drainage 15 of Sabinal River, *Smith 678* (LL); Lost Maples State National Area, *Snyder 274* (LL); Sabinal Canyon, ca. 7 mi. N of Vanderpool, 8 Apr. 1972, *Welborn s.n.* (TEX); Hwy. 407 (470?) between Utopia and Tarpley, S bank of Hondo Creek, 9 Apr. 1972, *Welborn s.n.* (TEX). Kendall Co.: ca. 6.5 mi. NW of Boerne, on tributary of Cibolo Creek, 24 Sep. 1983, *Breckenridge s.n.* (TEX); Spanish Pass, 5 July 1911, *Clemens & Clemens s.n.* (MO, POM, TEX); Boerne, 1911, *Hastings s.n.* (A); Boerne, *Palmer 9843* (GH, MO); Cibolo Creek, Boerne, *Palmer 11474* (GH, MO, NY); Cibolo, 15 June 1913, *Schattenberg s.n.* (A). Real Co.: along TX 337, 3 mi. W of Leakey, *Miller et al. 5145* (MO). Uvalde Co.: Garner State Park, SE boundary of park along Frio River,

Riskind 1691 (LL); Garner State Park, southern portion of park, 9 Apr. 1972, *Welborn s.n.* (TEX).

The range of *Styrax platanifolius* subsp. *stellatus* is contiguous with the southern boundary of subspecies *platanifolius*, occurring at the southern edge of the Edwards Plateau. It is rare throughout its range, with the exception of Sabinal Canyon State Park, where apparently populations are common and often composed of many individuals (*Riskind 1682*).

Gonsoulin (1974) incorrectly cited the holotype at TEX and an isotype at F.

14d. Styrax platanifolius subsp. **texanus** (Cory) P. W. Fritsch, comb. et stat. nov. Basionym: *Styrax texanus* Cory, Madroño 7: 112. 1943 ["*S. texana*"]. TYPE: U.S.A. Texas: Edwards Co., Polecat Creek, 4 July 1941, *V. L. Cory 34940* (holotype, GH). Figure 65.

Young twigs faintly glaucous, glabrous except for scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above glabrous, below thinly and evenly white-stellate-pubescent except for scattered orange-brown or dark brown stalked stellate hairs on some leaves, the surface completely covered and obscured by the pubescence, margin usually entire or weakly undulate, rarely lobed or coarsely toothed. Pedicel and calyx thinly and evenly white-stellate-pubescent. At least some calyx teeth to 1 mm long, the teeth and calyx margin densely glandular. Style pubescent from base to 15–35% of the total length.

Rare, occurring in west-central Texas on the Edwards Plateau escarpment; 500–700 m; steep limestone cliffs. Flowering: April–May; fruiting: July–September.

Common name. Texas snow-bell (Gonsoulin, 1974; Cox, 1987).

Additional specimens examined. UNITED STATES. **Texas:** Edwards Co.: Cedar Creek, canyon walls above perennial springs, 25 Sep. 1983, *Breckenridge s.n.* (TEX); Polecat Creek, 4 July 1940 or 1941, *Cory s.n.* (GH, RSA), 19 Apr. 1942, *Cory s.n.* (GH, POM), *Cory 34937* (TEX), *Cory 34938* (POM), *Cory 34939* (TEX); Cedar Creek, 1.25 mi. above Roberts Creek, *Cory 37767* (TEX), *Cory 37769* (A); Cedar Creek, *Cory 38763* (TEX), *Cory 38764* (A); Polecat Creek, *Cory 38933* (TEX); Polecat Canyon, *Cory 38934* (NY); Little Hackberry Canyon, *Cory 42953* (NY); Little Hackberry Creek, 14.5 mi. E of Rocksprings, *Cory 42956* (TEX); Polecat Creek, *Cory 49179* (LL); cliff above Cedar Creek, NW of Barksdale, *Dorr & Nixon 1918* (TEX); Cedar Creek Canyon NW of Barksdale, *Johnston et al. 7428* (TEX); Jessup Ranch on Little Hackberry Creek, *Keeney 1456* (NY); Polecat Creek, *Keeney 1457* (MO). Real Co.: Nueces Canyon, 4.5 mi. N of Hackberry, *Cory 42659* (F), *Cory 42661* (TEX), *Cory 42664* (NY), *Cory 42666* (TEX); Nueces River, 4.25 mi. above Hackberry, *Cory 42668* (A), *Cory 42669* (POM); Nueces River, 1 1/3 mi. above Hackberry, *Cory 42673* (A), *Cory 42677* (NY), *Cory 42678* (F); 9 mi. ENE of Vance, W side of Bullhead Creek, *Johnston 7304* (TEX).

Styrax platanifolius subsp. *texanus* has the narrowest distribution of the five *S. platanifolius* subspecies, with documented localities in Edwards and Real Counties, Texas, and one population reported in Del Rio County, Texas. It is probably also the rarest of the subspecies, with only nine populations known, four of which consist of more than two individuals (J. Poole, Texas Parks and Wildlife Department, Austin, Texas, pers. comm.). Although seed production and the germination rate of *S. platanifolius* subsp. *texanus* are relatively high, grazing by both native and exotic herbivores has prevented regeneration within populations (Cox, 1987). Recovery efforts by the Texas Parks and Wildlife Department are under way to help ensure the survival of this taxon.

Gonsoulin (1974) incorrectly cited the type as "*Cory* 19 Apr 1942" with isotypes at GH and NY.

14e. Styrax platanifolius subsp. **youngiae** (Cory) P. W. Fritsch, comb. et stat. nov. Basionym: *Styrax youngiae* Cory, Madroño 7: 113. 1943 ["*S. Youngae*"]. TYPE: U.S.A. Texas: Limpia, canyon (on MO specimen only), Davis Mountains, 12 May 1914, *M. S. Young s.n.* (holotype, TEX; *M. S. Young 23* isotype, MO). Figures 55, 56, 66.

Young twigs densely white-stellate-pubescent in addition to scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above with scattered stellate pubescence, the hairs with 6–14 arms, below with a thick layer of white stellate pubescence except for scattered orange-brown or dark brown stalked stellate hairs on some leaves, the surface completely covered and obscured by the pubescence, the hairs of variable length, margin entire, undulate, or coarsely toothed. Pedicel and calyx with a thick layer of white stellate pubescence, the hairs of variable length. Calyx teeth to 0.6 mm long, usually shorter, the teeth and calyx margin sparsely glandular. Style pubescent from base to 60–80% of the total length.

Rare, Davis Mts., Texas, and eastern slopes of Chihuahuan desert mountains in northern Coahuila; 900–2000 m; izotal vegetation (*Yucca, Nolina, Dasylirion* associates), piñon/juniper woodland, in canyons; found on limestone; according to Cory (1943), found on igneous substrates in the Davis Mts., Texas, but this needs confirmation. Flowering: April–May; fruiting: July–September.

Common name. Young's snowbell (Gonsoulin, 1974).

Additional specimens examined. MEXICO. **Coahuila:** 12 mi. E of Boquillas in Sierra del Carmen, *Henrickson 11499* (TEX), *Henrickson 11561* (TEX); 17 km N of Rancho, El Jardín, *Johnston et al. 11888* (CAS, F, LL, MO, NY); Mina El Popo, ca. 2 km S of Cañon El Diablo, *Johnston et al. 11925* (CAS, F, LL, MEXU, MO, NY); 1 km W of Rancho Lagunita, *Riskind & Patterson 1915* (TEX); Mpio. de Villa Acuña, Serranías del Burro, Rancho El Bonito, *Riskind 2079* (TEX); Sierra del Carmen, 1/2 mi. S from its junction with the main part of Cañón del Diablo, *Wendt et al. 148b* (TEX); Sierra del Carmen, in fork of Cañón del Diablo, *Wendt 582* (MEXU, TEX).

Styrax platanifolius subsp. *youngiae* occurs in the Davis Mountains, Texas, U.S.A., and the Sierra del Carmen and surrounding mountainous regions in the Chihuahuan Desert, Coahuila, Mexico. The type locality in the Davis Mountains ("Limpia; canyon") has not been rediscovered. The Davis range consists primarily of igneous substrates, so Cory (1943) presumed the type to have come from an igneous rather than a limestone substrate. This fact and the higher elevation at which this subspecies occurs were considered to be features that distinguish *S. youngiae* from *S. platanifolius* and *S. texanus*. However, all subsequent collections of *S. platanifolius* subsp. *youngiae* that indicate substrate have come from limestone, placing in doubt Cory's (1943) assumption of an igneous substrate for the type. The elevation difference is still a distinguishing feature, although it is not as wide as Cory reported: Cory described *S. platanifolius* (= *S. platanifolius* subspp. *platanifolius* and *stellatus*) and *S. texanus* (= *S. platanifolius* subsp. *texanus*) as occurring below 600 m, and *S. youngiae* (= *S. platanifolius* subsp. *youngiae*) as occurring above 1200 m; current estimates of elevation ranges (based on data from herbarium labels) are 200–700 m for subspecies *platanifolius*, *stellatus*, and *texanus* combined, and 900–2000 m for subspecies *youngiae*.

The holotype is without number, but the isotype (*Young 23*) is clearly part of the same collection as the holotype, as indicated by the identical dates, general locality, and stage of leaf development.

15. Styrax radians P. W. Fritsch, sp. nov. TYPE: Mexico. Jalisco: (Mpio. de) San Sebastián, Hacienda del Cura, Sierra Madre, 2 Jan. 1927, *Y. Mexía 1351* (holotype, CAS; isotypes, A, DS, F, GH, MICH, MO, NY, UNC not seen, US). Figures 25, 61–63.

Arbor sempervirens; *lamina* ovata-oblonga vel elliptica, interdum lanceolata vel suborbicularis, subtus alba-stellata-pubescens, ad tactum mollis, venis secondariis et tertiariis evidentibus; *calyx* stellata-pubescens; *corolla* alba, tenuis, petalis connatis usque ad marginem calycem, lobis in aestivatione valvatis, sub anthesi apertis, patentibus moderate vel late; *filamenta* staminum partibus distinctis 2.5–3.5 mm longis et ad margines ventrales pilis stellatis aequiliter dispersis instructa, aliter fere glabra ventraliter praeter ad apices, brachis pilorum plus minusve radiatis ex axibus centralibus; *connectivum* antherae loculos noncontractos non vel leviter superans; *stigma* 0.6–0.8 mm lata.; *drupae* longiores 9–13 × 5–7 mm.

Evergreen tree to 12(–20) m. Young twigs grayish white-stellate-pubescent, often mixed with tawny- or orange-brown stellate hairs; outer layer of older twigs not exfoliating. Petiole 9–17 mm long. Lamina chartaceous, (8.5–)11–15(–24) × 4–9(–11.5) cm, broadly ovate-oblong or elliptic, sometimes lanceolate or suborbicular, secondary veins 9–15; apex acute to rounded, rarely broadly cuspidate; base subrounded to rounded, rarely truncate, subcordate, or cuneate, often slightly attenuate, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute white stellate hairs and also larger, woolly, whitish hairs rendering the surface soft to the touch, the minute hairs absent from the primary through tertiary veins, thus rendering the vein surface easily visible, the soft larger hairs rarely absent; margin entire. Inflorescences axillary or false-terminal, racemose or especially the larger usually paniculate, the racemes or panicle branches 2–6 cm long, 2–14-flowered. Lower pedicels 3–8 mm long. Calyx 2.5–5 × 2.5–5 mm, cupuliform or conical-cupuliform, grayish green-stellate-pubescent, rarely also with scattered orange-brown stellate hairs; calyx teeth 5, to 0.4 mm long or absent, deltoid, the calyx margin truncate or sometimes concave between the teeth, inner margin often glandular. Corolla white, 5–15 mm long, petals connate up to the calyx margin distally; corolla lobes 5, valvate in bud, 4–14 × 1–3 mm, non-overlapping, moderately or widely spreading, thin, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0–4 mm long; distinct portion of filament 2.5–3.5 mm long, of equal width throughout, ventrally not auriculate, ± densely white-stellate-pubescent at the incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.7 mm long; anthers 2–6 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style pubescent from base to 40–85% of the total length; stigma 0.6–0.8 mm wide. Drupe 9–13 × 5–7 (wider when 2-seeded) mm (not including occasional beak), ovoid or narrowly ellip-

soid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Most common in Nayarit and extreme western Jalisco, but also in southern Sinaloa, southern Mexico, northern Guerrero, and Oaxaca, Mexico; 400–1400 m; *Quercus* savannas, *Quercus-Pinus* forests, ecotones between subtropical deciduous forest and tropical subdeciduous forest, tropical subdeciduous forests, tropical deciduous forests; found often in valley bottomlands or barrancas. Flowering: November–June; fruiting: February–July.

Common names. Aguacatillo (Oaxaca, *MacDougall H156*), azagar (Jalisco, *Vázquez & Guzmán 4164*), azajar (Jalisco, *Cárdenas et al. 79, Robles et al. 813*), cortapico (Jalisco, *Mexía 1351*), levadura (Nayarit, *Gentry & Gilly 10863*), mamuyo (Jalisco, *Cuevas & Rosales 1876*), zajar (Jalisco, *Santana et al. 4776*).

Uses. Wood is used for ox yokes, plows, and other purposes where durable, tough wood is desired (Jalisco, *Mexía 1351*).

Additional specimens examined. MEXICO. **Guerrero:** Tlalchapa, *Aguirre 100-51* (MEXU). **Jalisco:** ca. 35 km E of Cabo Corrientes, *Anderson & Anderson 6109* (MICH); El Tuito, 11.5 km al NW del pueblo por el camino a Ixtlahuahey, *Ayala 678* (F, MO, NY); 14 km W of Villa de Purificación, *Bullock 2024* (CAS); Cuautitlán, 2 km NE of El Durazno, *Cárdenas et al. 79* (WIS); Cabo Corrientes, 15–78 km SW of Puerto Vallarta, *Cochrane et al. 11942* (WIS); new dirt road from San Sebastián W of La Estancia, *Cochrane et al. 12047* (WIS); Mpio. de Purificación, El Ocotillo, 10–12 km al NE de Purificación, *Cuevas et al. 709* (WIS); 4–6 km al NE de Casimiro Castillo, *Cuevas et al. 2391* (WIS); 4–5 km al W de Casimiro Castillo, *De Niz et al. 23* (WIS); gorge of the Río Horcones, 27 km by road S from Puerto Vallarta, *Dieterle 4023* (MICH); center of El Durazno, *Iltis et al. 389* (WIS); 2–7 km ENE of El Durazno, *Iltis et al. 459* (WIS); Ayotitlán, *Judziewicz et al. 5212* (WIS); 7.6 km al E de la carretera Puerto Vallarta, *Lott 2540* (CAS, MICH, MO); ca. 4 km al N de El Tuito, *Magallanes 1534* (MEXU, TEX); 6 km al NE de La Cuesta, *Magallanes 3432* (MEXU, MICH, MO); 10 km up road 2.5 km NW of town of El Tuito, *Mayfield et al. 1632* (TEX); foothills of Sierra de Manantlán (ca. 40 km SE of Autlán), *McVaugh 23250* (MICH); 3–6 km above (N of) La Cuesta, *McVaugh 23415* (MICH); valley of a stream 5 km N of El Tuito, *McVaugh 25492* (MICH); 3–10 km generally E on the road to Mina del Cuale, *McVaugh 26376* (MICH); San Sebastián, trail to Las Mesitas, *Mexía 1861* (CAS, US); Cuautitlán, 1–2 km al SW de Telcruz, *Nieves 411* (WIS); 6 km al NE de Telcruz, *Nieves 546* (WIS); Cerro Huehuentón, *Pérez 814* (NY); along hwy. from Puerto Vallarta S to Chamela at Río Horcones, *Plowman 14547* (F); Mpio. de Cuautitlán, Río Ayotitlán entre Ayotitlán y Chancol, *Ramírez & Alcocer 477* (WIS); 6.5–7.5 km al NE de Cuautitlán, *Robles et al. 813* (WIS); 11 km al NE de Cuautitlán, *Santana & Guzmán 3303* (WIS); La Astilla, 6 km al NW de Minatitlán, *Santana et al. 4776* (WIS); Mpio. de Talpa de Allende, camino de Talpa a Cuale, 4 km después de Talpa, *Vázquez 1195* (WIS); 1–2 km al E del Tecolote, El Tecolote, Casimiro Castillo, *Vázquez & Guzmán 4164* (WIS). **México:** Mpio. de Temascaltepec, Luvianos, *Hinton 5309* (A, F, RSA), *Hinton et al. 6193* (CAS, NY, RSA, US); Mpio. de Temascaltepec, Villaneda, *Hinton et al. 7410* (A, MO, U, US); 3 mi. W of Luvianos, *Moran 10161* (DS, RSA). **Nayarit:** Camichín de Juaja, *Calzada 17840* (RSA); 4 km al NE del poblado de Sta. María del Oro, *Calzada et al. 18805* (MICH); Hwy. 28 between Tepic and Jalcatlán at km 14–16, *Croat 45262* (CAS, MO); 3 km al SW del Izote, camino al Cuarenteño, *Flores & Ruenes 1907* (F, MO); 11 km al W de Jalcocotán, *Flores & Ramírez 2498* (MICH, MO); 11 km al NE del Izote, camino a Palapita, *Flores-Franco et al. 3344* (MICH); 8 to 10 mi. W of Tepic, *Gentry & Gilly 10485* (LL, MICH); 15 mi. S of Tepic along hwy. to Compostela, *Gentry & Gilly 10811* (LL, MICH); 15 mi. S of Tepic along road to Compostela, *Gentry & Gilly 10863* (LL, MICH); mountains 9 mi. N of Compostela, *McVaugh & Koelz 541* (MICH); ca. 10 road-mi. E of Jalcocotán on road to Tepic, *McVaugh 12100* (MICH); 3 km NW of El Ocotillo, *McVaugh 23515* (MICH); along dirt road to Cuarenteño, 2–10 km from El Izote, *Miller & Téllez 3140* (CAS, MO); ca. 3 mi. E of Jalcocotán, *Norris 14959* (MICH); Rancho de la Siempreviva, *Ortega 60* (A, US); 2 a 10 km de Mazatan, *Ramírez & Flores 894* (MICH, MO); La Escondida, 14 km al NE de Tepic, *Téllez 10282* (MO); km 9.5 de la terraceria al Cuarenteño, *Téllez et al. 10412* (MICH, MO); between Tepic and Ixtlán del Río, 14 Nov. 1953, *Templeton s.n.* (RSA), *Templeton 7000* (RSA); 2 km al NE del Izote, Cerro San Juan, *Tenorio et al. 15605* (MICH, MO, RSA); 68 km al NE de San Pedro Ixzcatán, *Tenorio et al. 16929* (MICH, MO); 3 km al S del Izote, *Tenorio et al. 16984* (MICH, MO); Volcán Sanganguey, Tepic, *Walker 73H07* (NY). **Oaxaca:** Mpio. de San Jerónimo Coatlán, 38.6 km al SW de San Jerónimo Coatlán, *Campos 3467* (MEXU); Arroyo Limón, San Vincente, Putla, *MacDougall H155* (F, NY); San Vincente, Putla, *MacDougall H156* (F, NY); vicinity of Concordia, Pochutla, *Makrinus 551* (US); Cafetal Concordia (Cerro Espino), *Reko 3642* (US); Mpio. de San Mateo Pinas, 2 km de Cafetitlan, *Saynes 1437* (MEXU). **Sinaloa:** Mesa Malqueson, Cerro Colorado, *Gentry 5164* (DS, F, MEXU, MICH, MO, NY, RSA); El Agua Colgada, San Ignacio, *Montes 714* (US); San Juan, *Ortega 4118* (US); Mazatlán, *Ortega 5082* (BH, US); La Copetona, Arriba de Guadalupe de Los Reyes, *Tenorio 8364* (RSA, TEX); San Juan 14 km al SE de San Ignacio, *Tenorio 8441* (RSA).

Styrax radians is a relatively common and widespread species, occurring at mid elevations along the western escarpment of the Sierra Madre Occidental and the southern slopes of the trans-Mexican volcanic belt in Mexico. It appears to be most common in the states of Jalisco and Nayarit. The species occurs in three disjunct areas: Sinaloa to southern Jalisco, northern Guerrero and the southern portion of the state of México, and southern Oaxaca. The disjunction between western Mexico and eastern Mexico is likely to be real rather than an artifact of inadequate collecting because numerous collections of *Styrax*, especially *S. ramirezii*, have been made in the intervening areas. Plants occurring in the eastern part of the range have leaves that are a little larger on average than those

in the west, but they are otherwise essentially indistinguishable. Some populations in western Mexico have extremely small flowers, but this is only an extreme form of a completely continuous character and cannot be used for the designation of infraspecific taxa.

Perkins apparently did not see any collections of this species. Gonsoulin (1974) considered the collections placed here in *S. radians* to fall within the range of morphological variation exhibited by *S. argenteus* var. *argenteus*. However, *S. radians* is easily distinguishable from *S. argenteus* by the non-tapered anther sacs, non-prolonged connectives, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. Furthermore, the ranges of the species overlap only in Oaxaca. *Styrax radians* can be distinguished from other sympatric species of *Styrax* by its evergreen habit, drupaceous fruit, stellate pubescence throughout, and corolla lobes that are united only to the calyx margin. Pubescence on the lower laminar surface, consisting of a short, dense tomentum and a longer tomentum soft to the touch, is usually a good character distinguishing sterile specimens of *S. radians* from *S. ramirezii*; in *S. ramirezii*, the lower laminar surface is usually at least somewhat rough to the touch. However, the soft tomentum is not always present in *S. radians*, and some specimens of the stellate form of *S. ramirezii* approach *S. radians* in this respect. In these cases, the lower elevation at which *S. radians* occurs (400–1400 m, usually below 1000 m) as compared to that of *S. ramirezii* (770–3100 m, usually above 1500 m) can aid in identification.

16. Styrax ramirezii Greenm., Proc. Amer. Acad. Arts 34: 568. 1899. *Styrax argenteus* var. *ramirezii* (Greenm.) Gonsoulin, Sida 5: 227. 1974. TYPE: Mexico. Morelos: Mountain canyons above Cuernavaca, 15 May 1898, *C. G. Pringle 6848* (holotype, GH; isotypes, A, BH, BR, F, MEXU, MO, NY, PH not seen, POM, US, W). Figures 3, 4, 8, 57, 67–70.

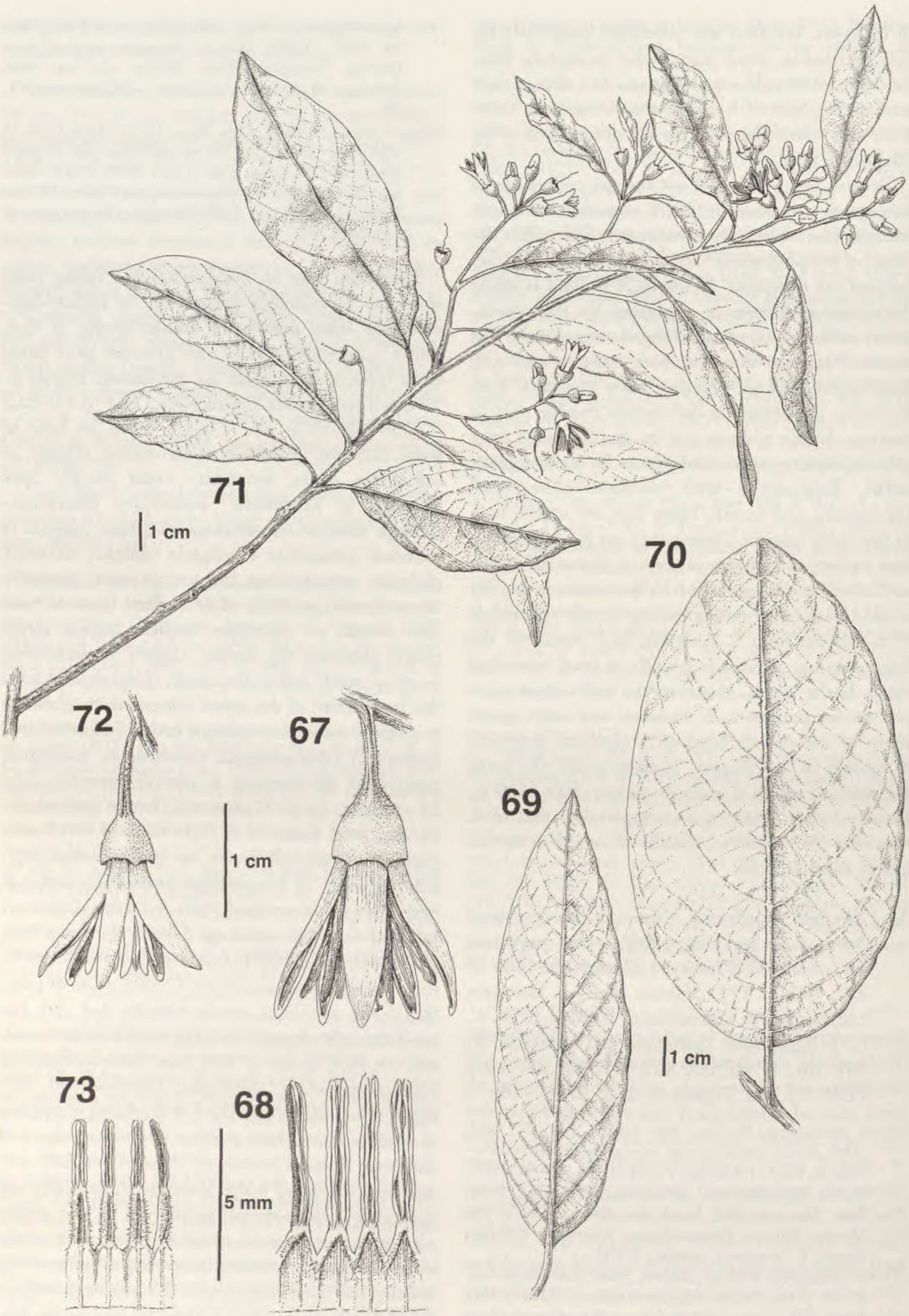
Styrax micranthus Perkins, Bot. Jahrb. Syst. 31: 480. 1902. *Styrax ramirezii* var. *micranthus* (Perkins) Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 54. 1907. *Styrax argenteus* var. *micranthus* (Perkins) D'Arcy, Ann. Missouri Bot. Gard. 66: 169. 1979. TYPE: Mexico. México: Temascaltepec, *Ehrenberg 498* (holotype, B destroyed; isotype, POM).

Styrax cyathocalyx Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906. TYPE: Mexico. Oaxaca: Rincón, May 1844, *H. Galeotti 1687* (holotype, B destroyed; photo of holotype, F, GH, US; isotypes, BR (2), G-DEL not seen, NY, US, W).

Styrax orizabensis Perkins, Repert. Spec. Nov. Regni Veg. 2: 25. 1906. *Styrax ramirezii* var. *orizabensis* (Perkins) Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 54. 1907. TYPE: Mexico. Veracruz (probably) or Puebla: Orizaba, 1856, *Botteri s.n.* or *1006* (holotype, B destroyed; isotypes, G-DC not seen, NY, W).

Styrax hintonii Bullock, Bull. Misc. Inform. Kew 1936: 9. 1936 ["*S. Hintoni*"]. *Styrax argenteus* var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974. TYPE: Mexico. México: Dto. de Temascaltepec, Calera, 19 Apr. 1933, *G. B. Hinton 3798* (holotype, K; isotypes, F, GH, MO, US).

Evergreen tree to 20(–25–27) m. Young twigs short- to long-stellate-pubescent, or radiate-lepidote, the hairs yellow- or orange-brown, or dark brown, sometimes mixed with greenish gray hairs; outer layer of older twigs not exfoliating. Petiole 5–25 mm long. Lamina chartaceous, (10.1–)11.0–22.5 × 2.9–9.5(–10.5) cm, 1.6–4.4 times as long as wide, narrowly or broadly ovate-oblong, elliptic, or sometimes ovate, secondary veins 10–15; apex rounded to acuminate, sometimes emarginate through abortive tip development; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with greenish white stellate hairs of variable length or sometimes radiate scales, rarely nearly glabrous, the surface slightly to moderately rough or rarely soft to the touch, if soft then at least the lower third of the calyx villous; veins glabrous to densely tomentose; margin entire. Inflorescences axillary or false-terminal, racemose or sometimes paniculate, the racemes or panicle branches 2.5–12 cm long, (2–)5–17-flowered. Lower pedicels 4–11 mm long. Calyx (1.5–)3–6 × (3–)3.5–6.5 mm, cupuliform, grayish green- or brown-radiate-lepidote, or short- to long-stellate-pubescent; scales at mid-calyx (when present) 0.05–0.17 mm diam.; calyx teeth 5, to 0.5 mm long, deltoid, the calyx margin slightly or distinctly concave between the teeth, inner margin often glandular. Corolla white or pink, (8–)11–14 mm long, petals connate 1–3 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 6–10 × 2–3 mm, non-overlapping, slightly spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 1–3 mm long; distinct portion of filament 0.6–2.0(–2.6) mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.3 mm long; anthers 3.0–4.8 mm long, 1.9–5.3 times as long as the distinct portion of the filaments, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style



Figures 67–73. 67–70. *Styrax ramirezii.* —67. Flower, *Pringle 9000* (MO). —68. Four adjacent stamens, *Hinton et al. 7605* (TEX). —69. Leaf of small-scaled form, *Pringle 9000* (MO). —70. Leaf of stellate form, *Koch & Sánchez 7929* (F). 71–73. *Styrax warscewiczii, Davidse 24632* (MO). —71. Flowering branch. —72. Flower. —73. Four adjacent stamens.

glabrous or pubescent at base only; stigma 0.3–0.5 mm wide. Drupe (7–)9–15 × 5–9 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Southern Sinaloa and Durango south to western Jalisco and northern Colima, east to northern Morelos and Oaxaca, and from the southern portion of the state of México south to central Guerrero; 770–3100 m; bosque mesofilo de montaña, *Quercus-Abies* forests, *Quercus-Pinus* forests, tropical semi-evergreen cloud forests, seasonally dry tropical subdeciduous forests; found often along waterways, sides of arroyos, humid canyons, deep riverbeds, disturbed situations, on granitic rock, rich soil, or sandy clay. Flowering: various times throughout year; fruiting: various times throughout year.

Common names. Azajar (Jalisco, *Niz et al. 290*), chilaquate (Morelos; Standley, 1924), escaramuza (Jalisco, *Mexía 1504*), garrapata (Michoacán, *Sharp 45499*), jaboncillo colorado (Michoacán, 17 Dec. 1971, *Rees s.n.*), mamullo (Jalisco, *Jardel et al. 214*), mamuyo (Jalisco, *Cuevas 1251, 1294,* and *1366*), memelita (Estado de México, *Hinton et al. 6145*), palo de casa (Jalisco, *Cevallos et al. 72, Muñoz & Vázquez 36*).

Additional specimens examined. Stellate form (selected specimens): MEXICO. **Guerrero:** Yesceros, *Hinton 14409* (GH, LL, RSA, US). **Jalisco:** San Sebastián, E of Arroyo Santa Gertrudis, *Méxia 1504* (A, CAS, DS, F, GH, MICH, MO, NY, US). **México:** Calera, Temascaltepec, *Hinton 7605* (A, DS, GH, LL, MICH, MO, RSA, TEX, US). **Michoacán:** Pontezuelas, 20 km al E de Morelia, *Rzedowski 18371* (DS, MICH, NY, TEX, US). **Nayarit:** base of Cerro Sanganguey, ca. 20 km SE of Tepic, *Miller 3114* (MO, TEX).

Large-scaled form: MEXICO. **Chiapas:** Paraje Vo'bits, *Laughlin 408* (DS, LL, US); 2 km camino Cabecera Zinacantan a pobablado Salinas, Zinacantan queda al W del pueblo, *Ton 9329* (CAS, TEX, WIS). **Oaxaca:** Dto. de Ixtlán, 6 km NNE of La Luz, *Boyle 3841* (MO); 20 km NE of Teotitlán del Camino, *Breedlove 59921* (CAS, NY); Mpio. de San Jerónimo Coatlán, 36 km al SE de Cruz de Honduras, *Campos 4740* (CAS, MEXU); Dto. de Cuicatlán, Cuyamecalco, *Conzatti 2338* (F); La Loma, Cuyamecalco, *Conzatti 2450* (F); 13 mi. E of Teotitlán, *Croat 48197* (MO); Mpio. de Comaltepec, S Comaltepec, *Hernández 322* (MEXU); Tonaguia, *Liebmann 596B* (F); Camino de Coyula a Cuyamacalco *Smith 347* (GH); Sierra Mazateca, Plan de Guadalupe, *Solheim 1397* (NY, WIS); 30 km al NE de Teotitlán, *Tenorio 14351* (MEXU, MO, RSA, TEX).

Small-scaled form (selected specimens): MEXICO. **Colima:** Mpio. de Minatitlán, Cerrito Breñoso, *Santana 2695* (MEXU). **Durango:** along the Mazatlán–Durango Hwy. 3–15 km toward El Salto from Sinaloa, *McVaugh 23593* (MICH). **Guerrero:** second ridge W of Petlacala, *Méxia 9059* (B, CAS, F, GH, LL, MO, NY, U, US). **Jalisco:** Rancho El Terrero, 1.5 km adelante del aserradero, *Flores 2680* (MEXU, TEX). **México:** 8 km al W de Cuernavaca, *Koch 7929* (CAS, F, MO, NY). **Michoacán:** San Felipe, Zitácuaro, *Hinton 11831* (F, GH, LL, MO, NY, US, W). **Morelos:** Sierra de Tepoxtlan, *Pringle 8023* (A, B, BH, BR, F, GH, MEXU, MO, NY, POM, US, W). **Sinaloa:** 1 mi. S of El Palmito on Hwy. 40, 1 mi. W of hwy., *Sanders 4405* (RSA, TEX).

Styrax ramirezii is one of the most common and widespread species treated in this revision. It is endemic to Mexico, occurring at relatively high elevations on the western slopes of the Sierra Madre Occidental from Sinaloa to Jalisco, the southern slopes of the trans-Mexican volcanic belt from Jalisco to Morelos, the Sierra Madre del Sur, the eastern escarpment of the Sierra Madre in Oaxaca, and rarely in the mountains of Chiapas. The distribution of this species shows a striking pattern along the trans-Mexican volcanic belt, essentially occurring only within a narrow band north of the Río Balsas basin.

This species exhibits a great deal of morphological variation across its range. The indumentum on the calyx can be of long or short stellate hairs, small or large radiate scales, or a mixture of these types. The pubescence on the lower laminar surface can consist of a thin to thick layer of long and/or short stellate hairs or radiate scales, or it may be nearly absent. The veins on the lower laminar surface are usually visible through any pubescence, but in most specimens from Oaxaca and Chiapas they are not. Scattered orange-brown stellate hairs or radiate scales sometimes occur on the calyx. Leaf and flower size varies a great deal throughout the range of the species.

Differences between *S. ramirezii* and other species of *Styrax* are addressed in the discussions under *S. argenteus, S. austromexicanus, S. magnus, S. radians,* and *S. warscewiczii.*

The extensive morphological variation exhibited by this species is often not random, either in terms of the correlations of characters or geographically, and this complexity is likely responsible for the contrasting treatments of *S. ramirezii* by Perkins (1907) and Gonsoulin (1974). Perkins (1907) defined *S. ramirezii* relatively narrowly, although her concept of this species was still broad enough to maintain three varieties within it (vars. *micranthus* and *orizabensis,* as well as the typical variety). She considered *S. cyathocalyx* and *S. warscewiczii* to be distinct species. Gonsoulin (1974), who had access to more material, considered the variation in most evergreen *Styrax* from Mexico as inconsequential or highly intergrading, and thus circumscribed *S. argenteus* var. *ramirezii* to include seven previously recognized taxa: *S. cyathocalyx, S. micranthus, S. orizabensis, S. polyanthus, S. polyneurus, S. ramirezii,* and *S. warscewiczii.* Gonsoulin (1974) consid-

Table 2. Mean and standard error (SE) of lamina length/width ratio (= 1/w) and elevation for four groups within *Styrax ramirezii* recognized on the basis of calyx trichome differences. Measurements were obtained from herbarium specimens. Lamina shape was estimated by dividing length by width (average of two largest leaves per collection, one duplicate sampled per collection; sample list available from the author upon request). N = sample size.

Group	1/w			Elevation (m)		
	N	Mean	SE	N	Mean	SE
stellate form	43	2.19	0.06	39	1903	51
stellate/small-scaled intermediates	10	2.49	0.12	9	1977	107
small-scaled form	79	2.82	0.04	64	2193	122
large-scaled form	12	2.82	0.11	7	2289	40

ered *S. hintonii*, a species described subsequent to Perkins's published research on the Styracaceae, to be a variety of *S. argenteus*, and treated *S. magnus* and *S. vulcanicola*, also described after Perkins's publications, as synonyms of this variety.

The present revision follows Perkins's (1907) concept of *Styrax ramirezii* more closely than that of Gonsoulin (1974). The species status of both *S. ramirezii* and *S. warscewiczii* is recognized, as in Perkins (1907). However, in contrast with Perkins (1907), *S. cyathocalyx*, *S. ramirezii* var. *micranthus*, and *S. ramirezii* var. *orizabensis* are reduced to synonymy under *S. ramirezii*. The present treatment is concordant with Gonsoulin (1974) in that *S. cyathocalyx*, *S. micranthus*, and *S. orizabensis* are treated as synonyms, but differs in that *S. ramirezii* and *S. warscewiczii* are treated as species, and *S. polyanthus* and *S. polyneurus* are placed in synonymy under *S. argenteus* and *S. warscewiczii*, respectively. Furthermore, *S. argenteus* var. *hintonii* is placed here in synonymy under *S. ramirezii*, and *S. magnus* is treated as a distinct species; *S. vulcanicola* is treated as a synonym of the latter name.

The present circumscription of *S. ramirezii* comprises three fairly distinctive infraspecific entities. One of these has scales at mid-calyx that are 0.15–0.17 mm diam. This "large-scaled" form occurs only in Oaxaca and Chiapas. Another form has scales at mid-calyx that are 0.05–0.12 mm diam. This "small-scaled" form is wide-ranging, occurring from Sinaloa to northern Morelos and the Sierra Madre del Sur. In a third form the calyx is stellate-villous on at least the lower third. This "stellate" form is also widespread, but occurs entirely within the range of the small-scaled form, from Nayarit to the southern portion of the state of México and the Sierra Madre del Sur. Specimens exhibiting calyx-trichome morphology intermediate between that of the small-scaled and stellate forms comprise about 10% of the collections of *S. ramirezii*; most often they are from western Mexico and the state of México. Twig pubescence of the three forms generally corresponds to the calyx pubescence: the twigs are stellate-villous in the stellate form, and radiate-lepidote or rarely short-stellate-pubescent in the small-scaled and large-scaled forms. Also, most specimens of the large-scaled form possess a thick, dense layer of stellate hairs or radiate scales, whereas the other two forms have a thin layer of stellate hairs or radiate scales. In the stellate form this pubescence is often mixed with variable amounts of larger, white, stellate and somewhat stiff hairs. The small-scaled form is especially prevalent in northern Morelos, where the stellate form does not occur, and also extends farther north in western Mexico than the stellate form. The large-scaled form is apparently allopatric with respect to the other two forms. It is somewhat disjunctly distributed in the mountains of Oaxaca and a small area west of San Cristóbal de Las Casas. In this region *S. ramirezii* is difficult to distinguish from *S. warscewiczii* if flowers are not available.

The stellate form of *S. ramirezii* in general possesses more broadly elliptic leaves and occurs at lower elevations than the small-scaled and large-scaled forms (Table 2). Analysis of variance tests showed significant differences among means of the three groups (level = 0.05) for the length:width ratio and elevation ($P < 0.001$ for both). The small-scaled and large-scaled forms did not differ significantly for length:width ratio or elevation in a post hoc comparison. To assess the distinctness of these forms, canonical discriminant analysis was performed with the computer program SYSTAT (Systat, Inc.). In this procedure, the proportion of individuals classified correctly by the discriminant function reflects its ability to distinguish among groups (see, e.g., Murrell, 1994). Mahalanobis distances (Sneath & Sokal, 1973) among the groups were significant [all P (univariate and multivariate) < 0.001] and the three groups were identified correctly $^{44}/_{64}$ (68.8%), $^{5}/_{9}$ (55.6%), and $^{28}/_{39}$ (71.8%) of

the time, respectively, on the basis of the discriminant function. Thus, the discriminant function showed that calyx trichome type tends to be associated with leaf shape and elevation differences.

Despite this general correspondence, however, formal recognition of the forms of *S. ramirezii* at the infraspecific level is not warranted, mainly because reliable key characters are lacking and there is a relatively high proportion of small-scaled and stellate intermediate forms scattered throughout the range of the stellate form. Furthermore, in Jalisco and Nayarit intermediates seem to be of a different nature from those in other areas in that they possess short-stellate hairs and narrowly elliptic leaves (e.g., *Miller 3114, Téllez 10139*); other intermediates seem to have the calyx and leaf characters combined more or less independently (especially collections near Nanchititla, in the state of México, e.g., *Bartholomew 2914*). More detailed studies focusing on associations between morphological and molecular variation, as well as differences in elevation and habitat, would shed further light on the ecology and population genetics of these forms.

I have placed *Styrax cyathocalyx* in synonymy under *S. ramirezii* with some hesitation. Perkins (1907) maintained the two species on the basis of differences in the size of the flowers: 1 cm long in *S. cyathocalyx* and 1.5–2 cm long in *S. ramirezii. Styrax cyathocalyx* was based solely on *Galeotti 1687.* The duplicates that I have seen of this collection possess floral buds and no flowers at anthesis; presumably Perkins had mature flowers available to her, because she described the corolla as 1 cm long, whereas the longest buds I could measure were only 0.6 cm long. If Perkins's observation is correct, the corollas are unusually short for *S. ramirezii.* The calyx (2 mm long) is also short, especially relative to the unusually long pedicels (14 mm). Perkins (1906) also described the style as denticulate, but expressed uncertainty as to whether this was an artifact or real. In the specimens I examined, the style margins are entire, i.e., in no way do they differ from those of other specimens of *Styrax.* A fruiting specimen from the same area in Oaxaca (*Liebmann 596B,* Tonaguia, Oaxaca) shows the same calyx and pedicel characters, and the fruit is unusually small (7 × 5 mm) for *S. ramirezii.* It is therefore possible that these collections represent a distinct variety of *S. ramirezii,* or even a distinct species. More collections of evergreen *Styrax* from Oaxaca, especially in flower, are needed before a conclusive taxonomic decision regarding the status of *S. cyathocalyx* can be reached. It would be especially helpful to rediscover populations at sites where Galeotti and Liebmann collected.

Perkins (1902) listed only *Ehrenberg 498* in the protologue of *S. micranthus*; the location of original material was not precisely indicated. From the protologue of *S. ramirezii* var. *micranthus* in Perkins (1907) it can be inferred that this collection was deposited at B and/or W. Because no material of *Ehrenberg 498* occurs at W, however, it is reasonable to assume that the holotype was at B, and has been destroyed. The location of the original material of 15 species described in the publication that included *S. cyathocalyx* and *S. orizabensis* (Perkins, 1906) was indicated only vaguely as existing partly at B, BR, G-BOIS, G-DC, P, and/or W. I have assumed that the holotypes of these two species names were located at B, because that is where Perkins conducted her work; they have in all likelihood been destroyed. See the discussion under *S. glabrescens* for information concerning the collection date of *Galeotti 1687.*

When Gonsoulin (1974) made the combination *Styrax argenteus* var. *ramirezii,* he listed *S. micranthus* Perkins as a synonym. The latter name is the basis of *S. ramirezii* var. *micranthus* (Perkins) Perkins (1907), making Gonsoulin's varietal name superfluous. D'Arcy (1979) corrected Gonsoulin's error by making the combination *S. argenteus* var. *micranthus.*

The protologue of *Styrax ramirezii* Greenm. (Greenman, 1899) does not specify the holotype location. The NY duplicate of *Pringle 6848* is cited as the holotype of *S. ramirezii* in Gonsoulin (1974). However, Greenman worked at GH until 1899, studied at the University of Berlin from 1899 to 1901, and returned to GH in 1902 (Woodson, 1951). On this basis, I consider it best to regard the GH specimen as the holotype. Gonsoulin (1974) also cited the MO duplicate of *Hinton 3798* as the holotype of *S. hintonii.* However, Bullock worked at K, so the specimen there should be regarded as the holotype.

17. Styrax steyermarkii P. W. Fritsch, sp. nov. TYPE: Guatemala. Baja Verapaz: Unión Barrios, E of km 154, 16 Apr. 1975, *C. L. Lundell & E. Contreras 19214* (holotype, CAS; isotypes, LL, MEXU, MO, NY). Figures 6, 22–24, 47.

Arbor sempervirens; *lamina* 2.1–3.0plo longior quam latior, subtus pilis densis stellatis instructa; *calyx* radiatus-lepidotus, squamis densis cinerascentibus-viridis et saepe dispersis ferrugineis ad medicalycem 0.13–0.25 mm diam. instructus; *corolla* lobis in aestivatione valvatis, sub anthesi apertis, linearibus; *filamenta* staminum partibus distinctis ad margines ventrales auriculatis, auriculis pilis albis-stellatis dense instructis, brachis pilorum usque ad 1.5 mm longis, illis pilorum apicem versus pro parte

maxima ordinatis apicem floralibus versus; *antherae* 4.5 mm longae; *connectivum* antherae loculos contractos manifeste superans.

Evergreen tree to 20 m. Young twigs grayish green- to dark orange-brown-radiate-lepidote; outer layer of older twigs not exfoliating. Petiole 9–20 mm long. Lamina chartaceous, 11–16 × 3.5–7.5 cm, 2.1–3.0 times as long as wide, elliptic, secondary veins 6–8; apex acute to abruptly short-acuminate; base cuneate, rarely subrounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute grayish green stellate hairs and sparsely scattered, larger, grayish green or orange-brown stellate hairs or radiate scales, the latter particularly prevalent near and on the veins; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 2.5–4 cm long, (1–)4–7-flowered. Lower pedicels 5–8 mm long. Calyx 2.5–3 × 4 mm, conical-cupuliform, in fruit shallowly cupuliform, grayish green-radiate-lepidote, sometimes with scattered orange-brown radiate scales toward the base; scales at mid-calyx 0.13–0.25 mm diam.; calyx teeth 5, to 0.3 mm long, linear, the calyx margin slightly concave between the teeth, inner margin often glandular. Corolla white, 12–15 mm long, petals connate up to the calyx margin distally; corolla lobes 5, valvate in bud, 10–12 × 2 mm, non-overlapping, spreading, slightly thickened, linear, vesture on the outer distal third of the lobes consisting of radiate scales. Free portion of stamen tube 1 mm long; distinct portion of filament 2–3 mm long, of equal width throughout, ventrally with auricles bearing a dense mass of stiff white stellate hairs with arms to 1.5 mm long, the hairs nearest the distal end of the filament with arms predominantly pointing upward, also pubescent below the auricles and at the sinus between adjacent filaments; anthers 4.5 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely short-stellate-pubescent; style glabrous or pubescent at base only; stigma 0.3 mm wide. Drupe 16–18 × 9–11 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens; fruiting calyx shallow, to 1.5 mm long. Seed coat glabrous.

In the mountains of Guatemala, departments of Baja Verapaz, Huehuetenango, and Suchitepéquez, and in the Cordillera Talamanca in Costa Rica; 1500(–2600?) m; "in high forest on top of hill" (*Lundell 19214*), riverbanks. Flowering: March, June, July; fruiting: April.

Additional specimens examined. COSTA RICA. **Puntarenas:** Buenos Aires, Ujarrás, Quebrada Dorora, *Herrera 5866* (CAS, CR). GUATEMALA. **Baja Verapaz:** Niño Perdido, *Lundell & Contreras 21219* (LL). **Huehuetenango:** Cerro Huitz, between Mimanhuitz and Yulhuitz, *Steyermark 48666* (F); Maxbal, ca. 17 mi. N of Barillas, *Steyermark 48848* (F). **Suchitepéquez:** Volcán Santa Clara, *Holdridge 2299* (US).

Styrax steyermarkii is rare in the high mountains of Guatemala and Costa Rica. It is named after Julian A. Steyermark (1909–1988), prolific collector of the Guatemalan flora, as well as that of Missouri and of Venezuela, who first found the species in 1942.

This species is similar to *Styrax glabratus* by virtue of its radiate-lepidote calyx and stiff, long-armed, upward-pointing hairs on the stamen filaments ventrally, but differs most obviously from this species in its densely pubescent, as opposed to nearly glabrous, lower laminar surface. Gonsoulin (1974) mistook *S. steyermarkii* for *S. argenteus* var. *ramirezii*, most likely because the lepidote calyx and general appearance are very similar to that of *S. warscewiczii*, which he had placed in synonymy under variety *ramirezii*. However, the flower buds on *Steyermark 48666* clearly exhibit the stiff, long-armed, upward-pointing hairs on the stamen filaments ventrally, which are absent in *S. warscewiczii*, and the leaves are larger.

The closest relatives of *S. steyermarkii* appear to be several species from Andean South America. These include *S. buchtienii* Sleumer, *S. ferax* J. F. Macbr., *S. heterotrichus* Perkins, *S. leptactinosus* Cuatrec., *S. pentlandianus* Remy, *S. socialis* J. F. Macbr., and *S. subheterotrichus* Herzog. The taxonomy and relationships of these species are uncertain, but their types share with *S. steyermarkii* the lepidote calyx and lower laminar surfaces that possess either stellate hairs throughout or a mixture of stellate and scale-like hairs. *Styrax steyermarkii* can be distinguished from all these species by the longer upward-pointing stellate hairs on the stamen filaments ventrally, and by the possession of narrower anther connectives. These species plus *S. steyermarkii* (= the *S. steyermarkii* group) appear to be allied to the *S. ovatus* group, i.e., those species with peltate or lacerate-margined scales covering the leaves, stems, and calyces (including *S. conterminus, S. cordatus, S. leprosus, S. ovatus*, and *S. peruvianus*). Some of the species in the *S. steyermarkii* group appear to be polymorphic for the strongly peltate scales represented by the *S. ovatus* group and the radiate-lepidote scales found within most individuals of the *S. steyermarkii* group. A clearer understanding of the taxonomy and phylogeny of these groups and their phylogenetic positions

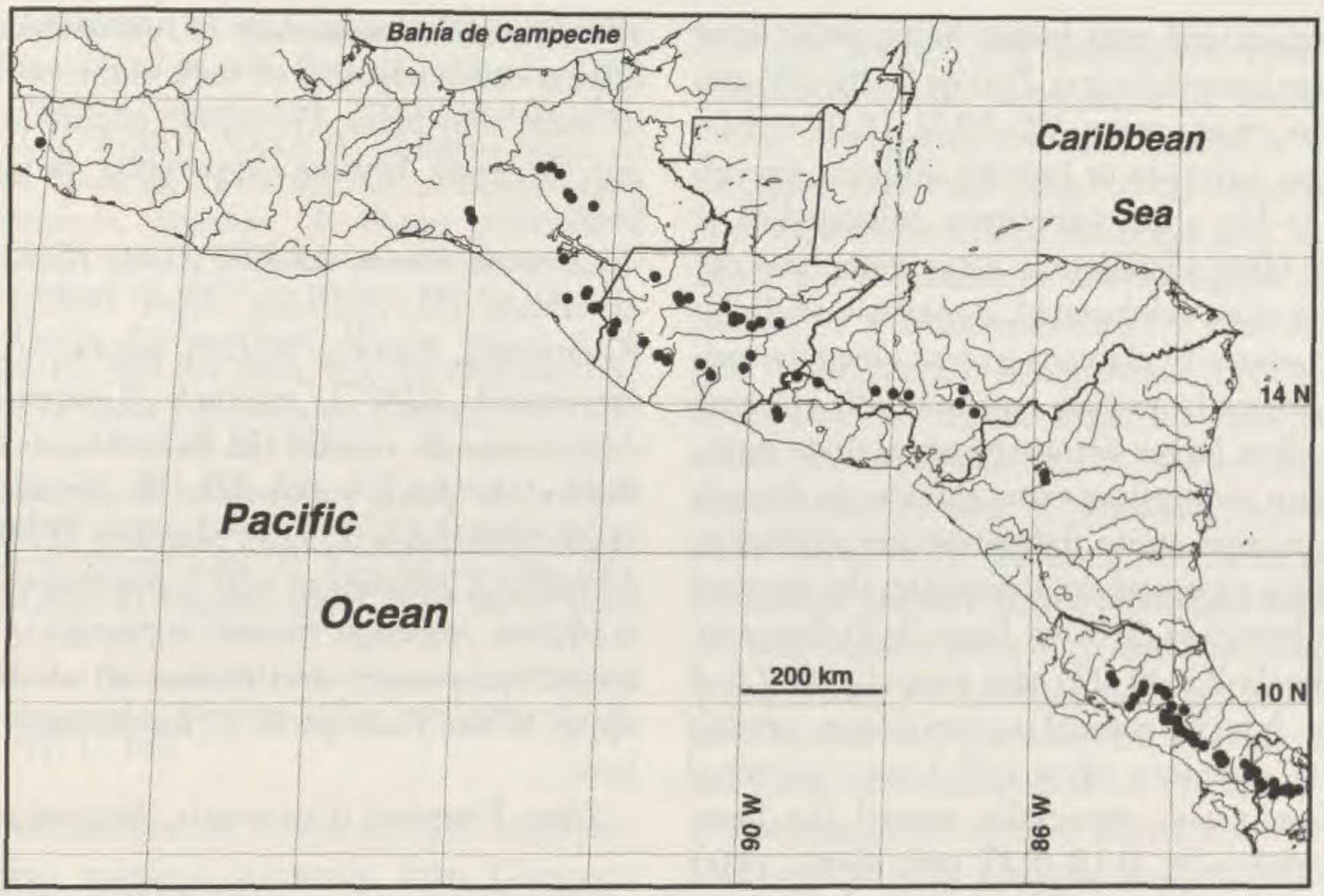


Figure 74. Distribution of *Styrax warscewiczii.*

within *Styrax* must await more detailed study of *Styrax* in South America.

18. Styrax tuxtlensis P. W. Fritsch, sp. nov. TYPE: Mexico. Veracruz: Los Tuxtlas Range, Mpio. de Mecayapan, Volcán Santa Marta, 18 May 1986, *J. V. LaFrankie 1306* (holotype, CAS; isotypes, GH, MO, TEX). Figures 25, 45, 46.

Arbor sempervirens; *lamina* lanci-ovata stellata-pubescens, basi manifeste obliqua; *inflorescentiae* ignotae; *calyx* stellatus-pubescens; *flores* ignoti; *drupa* angusta-ellipsoidea, 15–18 × 8 *mm*.

Evergreen tree to 10 m. Young twigs dark orange-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 9–11 mm long. Lamina chartaceous, 7.5–10 × 3.3–3.7 cm, lance-ovate or lanceolate, secondary veins 7–10; apex gradually or abruptly short-acuminate; base distinctly oblique and slightly attenuate; adaxially glabrous except along the major veins; abaxially covered with olive-gray stellate hairs and scattered orange-brown stellate hairs, the latter particularly prevalent near and on the veins; margin entire. Inflorescence and flowers unknown. Corolla presumably valvate in bud, non-overlapping at anthesis. Infructescences axillary or false-terminal, racemose, 3–5 cm long, with about 3–6 peducles or peduncle scars. Peduncle 5–6 mm long. Fruiting calyx 2–3 mm high, shallowly cupuliform, slightly concave between the 5 minute (0.25 mm long) teeth, the exterior surface densely covered with appressed stellate or scale-like hairs, inner calyx margin glandular. Drupe 15–18 × 8 (if 1-seeded) or 12 (if 2-seeded) mm, narrow-ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Known only from the type locality on Volcán Santa Marta in the Tuxtlas range, Veracruz, Mexico; 800 m; steep volcanic slopes. Fruiting: May.

This species is known only from one fruiting collection. It can be distinguished from all other species treated here by the distinctly oblique leaf bases. *Styrax tuxtlensis* is apparently geographically isolated from all other *Styrax* species except *S. glabrescens,* from which it can be easily distinguished by its evergreen habit and drupaceous fruit. More collections of this unusual species, especially in flower, are needed to better understand its taxonomy and relationships.

19. Styrax warscewiczii Perkins, Bot. Jahrb. Syst. 31: 480. 1902. TYPE: Costa Rica or Panama. "Veragua," (1848?), *Warscewicz 203* (holotype, B destroyed; photo of holotype, GH, MICH, US; isotype, F). Figures 5, 9, 10, 71–74.

Styrax polyneurus Perkins, in Donn. Sm., Bot. Gaz. 35: 5. 1903. TYPE: Costa Rica. [San José:] "In silvis ad Copey" (protologue), Feb. 1898 (protologue; "1896"? from US specimen), *Tonduz 11744* (holotype, B destroyed; isotypes, CR, F, US).

Evergreen tree to 20(–30) m. Young twigs stellate-pubescent, the hairs usually orange-brown, sometimes yellow-brown or dark brown, rarely

greenish gray mixed with brown hairs; outer layer of older twigs not exfoliating. Petiole 5–20(–25) mm long. Lamina chartaceous, 5.2–12.5(–16.0) × 1.6–4.5(–5.4) cm, narrowly or broadly elliptic, secondary veins 9–12; apex sometimes subrounded or acute, more often cuspidate to acuminate; base cuneate or less often subrounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially thickly covered with greenish white and often larger orange-brown stellate hairs, the secondary and tertiary veins glabrous to densely tomentose; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 2–6 cm long, 2–21-flowered. Lower pedicels 2.5–8(–11) mm long. Calyx 2.5–4 × 3–5 mm, broadly conical or cupuliform, grayish green-radiate-lepidote, often with larger, scattered orange-brown scales especially toward the base; scales at mid-calyx 0.13–0.33 mm diam.; calyx teeth 5, to 0.5 mm long, deltoid, the calyx margin concave between the teeth, inner margin often glandular. Corolla usually pink, sometimes white, sometimes white with pink lobes, 9–17 mm long, petals connate (0–)2–6 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 6–13 × (1–)1.5–2.5(–2.9) mm, non-overlapping, spreading or nearly erect, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of radiate scales. Free portion of the stamen tube 1–3 mm long; distinct portion of filament (1.0–)1.3–2.5 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with radiate arms to 0.3 mm long; anthers 1.7–3.6 mm long, 1.1–2.2 times as long as the distinct portion of the filaments, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3–0.4 mm wide. Drupe 7–12(–15) × 4–7(–8) mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Far western Panama north to western Chiapas, Mexico, disjunct to Guerrero in the Sierra Madre del Sur. One specimen collected from San Luis Potosí in the Sierra Madre Oriental, Mexico, is of uncertain status but resembles *S. warscewiczii*; most common from Chiapas to Guatemala, and in the Costa Rican cordillera; 1100–3200 m; cloud forests, *Quercus-Pinus* forests (Guerrero, Chiapas), lower montane wet forests, montane rainforests, dry montane forests, pastures, savannas; found in primary or secondary growth, in valleys and along streams, in the understory to unshaded, open situations, and roadsides, on rock outcrops, lava flows, or heavy clay loam. Flowering: apparently throughout the year; fruiting: apparently throughout the year.

Common names. Azulillo (Costa Rica, *Madriz 9*), el común (El Salvador, *Allen 6882*), estoraque (Guatemala, *Standley 58420*), estorace (Guatemala, *Steyermark 32827*), *estorach* (Guatemala, *Lamb 115*), oreja de venado (El Salvador, 4 June 1976, *Reyna s.n. p.p.*), sapuyulillo de montaña (Guatemala, *Steyermark 33315*). Standley (1938) has listed under *S. polyneurus* and *S. warscewiczii* the Costa Rican common names aguacate ascá, ascá, laurel, quiquicirrí, and resina, all of which likely apply to the concept of *S. warscewiczii* presented here.

Uses. Firewood (Guatemala, *Steyermark 33315*).

Selected specimens examined. COSTA RICA. **Alajuela:** Cinco Esquinas de Carrizal, *A. Jiménez 3653* (CR, F, MO). **Cartago:** Guarco, *Madriz 9* (CR, F, NY); near El Cañón, 40 km S of Cartago, *Williams et al. 28194* (F, NY, US). **Guanacaste:** Las Nubes, *Valerio 1396* (F). **Heredia:** S slope of Volcán Barba, *Hatheway 1258* (CR, DS, DUKE, F, GH, US). **Limón:** Valle de Silencio, *Davidse et al. 28606* (CAS, CR, DUKE, MO, NY). **Puntarenas:** Cantón de Buenos Aires, Ujarrás, El Carmen, Cerro Betsú, *I. Chacón 494* (CR, F, MO); Sitio Cotón (Cotonsito), along the road to Sitio Coto Brus, *Davidse 24632* (CR, MO). **San José:** overlooking the village of Boquete and about 20 km N of San Isidro del General, *Wilbur 21135* (AAU, BR, CAS, CR, DUKE, F, LL, MICH, MO, NY, TEX, US). EL SALVADOR. **Chalatenango:** Los Esesmiles, E of La Palma, *Allen & van Severen 7314* (F, GH, LL, NY, US). **Santa Ana:** Cerro Verde, *Allen 6853* (F, US); northern slopes of Volcán Santa Ana, *Allen 6882* (F, US); Cerro Montecristo, 4 June 1976, *Reyna s.n. p.p.* (CR). GUATEMALA. **Alta Verapaz:** Río Frío, entre Tactic y Santa Cruz, *Molina & Molina 12236* (F, NY, US). **Baja Verapaz:** Sierra de las Minas E of Chilascó, *Lamb 115* (F); Niño Perdido, *Lundell & Contreras 20452* (CAS, LL, MEXU, MO, NY). **El Progreso:** hills between Finca Piamonte, *Steyermark 43410* (F). **Escuintla:** forest vicinity of Volcán Pacaya, *Molina & Molina 27644* (F, MICH, U). **Guatemala:** upper slopes of Volcán Pacaya, *Harmon 4160* (MO, NY); Volcán de Pacaya, above Las Calderas, *Standley 58420* (A, F). **Huehuetenango:** trail between Ixteapoc and Soloma, *Steyermark 48441* (A, F). **Jalapa:** Volcán Jumay, N of Jalapa, *Steyermark 32340* (F, US); Monataña Miramundo between Miramundo and Buena Vista, *Steyermark 32827* (A, F). **Quezaltenango:** Quebrada San Gerónimo, Finca Pirineos, *Steyermark 33315* (F). **Quiché:** Nebaj, ca. 6 km SW.W, *Contreras 5102* (DS, F, LL, US). **Sacatepéquez:** hills of Finca Carmona, SE of Antigua, *Standley 63714* (A, F, NY). **San Marcos:** Volcán Tajumulco, SW of Tajumulco, *Steyermark 36712* (F). **Sololá:** Volcán Atitlán, *Steyermark 47397* (A, F). **Suchitepéquez:** Volcán Santa Clara, between Finca El Naranjo and upper slopes, *Steyermark 46759* (A, F). **Zacapa:** upper reaches of Río Sitio Nuevo, *Steyermark 43199* (F). HONDURAS. **El Paraíso:** Mt. Yuscarán, *Molina 627* (F). **Intibuca:** Cerca de Yashse, *Molina 6522* (F, GH, US). **La Paz:** Pinares del

Huis, *Molina 6460* (F, US). **Morazán:** San Juancito, *Williams & Molina 13318* (F, GH, MO, US). **Olancho:** trail between La Chorrera campsite and 1900 m camp on ridge, *Thomas et al. 474* (MO). MEXICO. **Chiapas:** Mpio. de Motozintla de Mendoza, 45–50 km NE of Huixtla along road to Motozintla, *Breedlove & Thorne 30989* (DS, DUKE, F, MEXU, MICH, NY); Barranca Honda near Siltepec, *Matuda 4135* (A, DS, LL, MEXU, MICH, NY, US). **Guerrero:** Piedra Ancha, Puerto Hondo, *Hinton et al. 14742* (F, GH, LL, MO, NY, RSA, US, W). **Oaxaca:** Dto. de Cuicatlán, La Loma Cuyamecalco, *Conzatti 3465* (US). **San Luis Potosí:** Río de las Gallinas, Rascon, *Purpus 5317* (CAS, F, GH, MO, NY, US). NICARAGUA. **Jinotega:** along Hwy. 3, ca. 1 km NW of La Fundadora entrance, *Miller & Stevens 1402* (DUKE, MEXU, MO, NY). **Matagalpa:** Cerro El Picacho above Hotel Santa María de Ostuma, *Nee 27636* (DUKE, LL, MO, NY). PANAMA. **Bocas del Toro:** Valle de Silencio, *Antonio 1640* (MO). **Chiriquí:** along road to Bambito, *Allen 4851* (BR, F, GH, MICH, MO, NY, U, US).

Styrax warscewiczii is a widespread, relatively high-elevation species, occurring from Guerrero, Mexico, to northern Panama. A collection of *Styrax* from San Luis Potosí may be this species as well (see below). In Mesoamerica, it is the species that generally replaces the equally common *S. argenteus* above 2000 m. It is most common in Chiapas and Central America; in Mexico west of Chiapas *S. warscewiczii* has been collected only once, in the Sierra Madre del Sur, Guerrero.

Gonsoulin (1974) placed this species in synonymy under *S. argenteus* var. *ramirezii.* His annotations of specimens referred to here as *S. warscewiczii* are usually *S. argenteus* var. *ramirezii,* but five are annotated as *S. argenteus* var. *argenteus,* and six as "intermediates" of varieties *argenteus* or *ramirezii. Styrax warscewiczii* is easily distinguished from *S. argenteus* as circumscribed in the present revision by the lack of both auricles and stiff, long-armed, upward-pointing hairs on the stamen filaments ventrally, as well as by the presence of radiate scales rather than stellate hairs on the calyx.

Styrax warscewiczii and *S. ramirezii* are morphologically similar in many respects. Nonetheless, they exhibit enough differences throughout their ranges to justify the recognition of these two entities as species, although they are likely to be closest relatives. They can be diagnostically differentiated from each other by vesture on the outer distal third of the corolla lobes, which consists of stellate hairs in *S. ramirezii* and radiate scales in *S. warscewiczii.* The two species can be further distinguished by the other characters in couplet 18 of the key: the anthers are longer and the ratio of anther length to the length of the distinct portion of the filaments is higher in *S. ramirezii.* Besides the characters listed in the key, *S. warscewiczii* differs from *S. ramirezii* by a tendency toward smaller leaves, smaller flowers, and shorter leaf internodes. However, these characters exhibit some degree of overlap.

The two species are most similar in Oaxaca and Chiapas, where the range of the large-scaled form of *S. ramirezii* overlaps the range of *S. warscewiczii.* There are a number of morphological patterns exhibited by *S. warscewiczii* and *S. ramirezii* that suggest bidirectional introgression between the two species in this region. First, the sizes of the calyx scales are equivalent in *S. warscewiczii* and the large-scaled form of *S. ramirezii,* whereas in the other forms of *S. ramirezii* the calyx pubescence consists of smaller scales or stellate hairs. Second, the large-scaled form of *S. ramirezii* exhibits a tendency toward the anther length and anther-filament ratio typical of *S. warscewiczii,* whereas in the other two forms of *S. ramirezii* these two characters clearly distinguish the species. Third, north of Honduras and especially in Chiapas many individuals of *S. warscewiczii* possess larger leaves and longer leaf internodes than is typical for the species, and thus the measurements of these characters approach or overlap those typical for *S. ramirezii.*

If these two species are in fact closest relatives, it may be difficult to ascertain whether the patterns of morphological variation displayed in the zone of sympatry are a result of primary speciation or secondary contact. A phylogenetic estimate that resolves the sister-group status of these species would make the pursuit of this issue practical. Further investigation of this problem should focus on the area of geographic overlap, especially where the two species apparently grow together in the area west of San Cristóbal de Las Casas in Chiapas.

Several other characters are variable across the range of *S. warscewiczii.* The southernmost populations (Costa Rica, Panama) tend to possess a higher percentage of brown versus grayish green radiate scales than those farther north. In Panama the radiate scales have somewhat longer arms (e.g., *Schmalzel 1608*). Character variation in some collections of *S. warscewiczii* (i.e., *Haber 357, Haber 2917, Haber 5541*) in extreme northern Puntarenas Province, Costa Rica (Monteverde and San Luis), suggests hybridization with *S. argenteus.* These collections have a mixture of grayish green radiate scales and nearly stellate hairs on the calyx. They were found at relatively low elevation and may grow with typical *S. argenteus,* which is known from the general area where these collections were made. The flowers do not deviate from the range of variation within *S. warscewiczii* as defined here. Additional study of individuals in this area is needed to establish whether these collections are hybrids or an unusual form of *S. warscewiczii.*

Two specimens from San José Province, Costa Rica (San Gerardo de Dota), here assigned to *S. warscewiczii*, have nearly glabrous abaxial leaf surfaces (*Kappelle MK118* and *MK1530*). These are the only specimens of this species that show this type of variation. The specimens are sterile. It is possible that they are hybrids between *S. warscewiczii* and *S. glabrescens*, the latter of which grows in the same area (cf. *Kappelle MK23*), but this is unlikely given the relatively great evolutionary distance between the two species. It is also possible that they represent an undescribed taxon.

A single collection of *Styrax* belonging to the neotropical evergreen group has been made in the state of San Luis Potosí, Mexico (*Purpus 5317*). Brandegee referred this collection to *S. polyneurus* (= *S. warscewiczii*); Standley (1924) thought that it might represent an undescribed species. The leaves of this collection are narrowly elliptic with the apex broadly acute or obtuse, and the leaf internodes are unusually short. In these respects it matches no other *Styrax* collection precisely. It is not a variant of *S. lanceolatus*, which occurs both north and south of the locality at which Purpus made his collection, because that species has a stellate-pubescent calyx and distinctive lanceolate leaves. The Purpus collection resembles *S. warscewiczii* in its large radiate scales on the calyx and small leaves (relative to *S. ramirezii*), so I have tentatively placed it in *S. warscewiczii*. However, the fact that this collection is so far removed geographically from any other collection of *S. warscewiczii* makes this placement uncertain. Until more material is available from the area, especially in flower, it will remain unclear whether *Purpus 5317* represents (1) an unusual form of *S. warscewiczii*, (2) a distinct infraspecific taxon of *S. warscewiczii*, (3) an intermediate between *S. warscewiczii* and *S. ramirezii*, or (4) a new species.

Excluded Names

Styrax diplotrichus Diels, Notizbl. Bot. Gart. Berlin-Dahlem 13: 508. 1937. TYPE: Mexico. Guerrero: Sierra Madre del Sur, Gipfel des Telpitzahua, *Jena 458* (holotype, B destroyed).

I have located no authentic material referable to this name. If the collection cited by Diels does not actually represent a new species, then on a geographical basis it could be a specimen of either *S. austromexicanus* or *S. ramirezii*. The description indicates that the leaves of the specimen are 7–9 cm wide, thus excluding *S. austromexicanus* from consideration. The description, although quite general, is not inconsistent with the characters of *S. ramirezii*. However, there is sufficient uncertainty to preclude the placement of this name in synonymy.

Styrax limoncillo (Humb. & Bonpl.) Miers, J. Linn. Soc., Bot. 17: 292. 1880. = *Symplocos limoncillo* Humb. & Bonpl.

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Numerical List of *Styrax* Species

1. *S. argenteus* C. Presl
2. *S. austromexicanus* P. W. Fritsch
3. *S. conterminus* Donn. Sm.
4. *S. gentryi* P. W. Fritsch
5. *S. glabratus* Schott
6. *S. glabrescens* Benth.
7. *S. incarnatus* P. W. Fritsch
8. *S. jaliscanus* S. Watson
9. *S. lanceolatus* P. W. Fritsch
10. *S. magnus* Lundell

11a. *S. nicaraguensis* P. W. Fritsch subsp. *nicaraguensis*
11b. *S. nicaraguensis* subsp. *ellipsoidalis* P. W. Fritsch

12. *S. panamensis* Standl.
13. *S. peruvianus* Zahlbr.

14a. *S. platanifolius* Engelm. ex Torr. subsp. *platanifolius*
14b. *S. platanifolius* subsp. *mollis* P. W. Fritsch
14c. *S. platanifolius* subsp. *stellatus* (Cory) P. W. Fritsch
14d. *S. platanifolius* subsp. *texanus* (Cory) P. W. Fritsch
14e. *S. platanifolius* subsp. *youngiae* (Cory) P. W. Fritsch

15. *S. radians* P. W. Fritsch
16. *S. ramirezii* Greenm.
17. *S. steyermarkii* P. W. Fritsch
18. *S. tuxtlensis* P. W. Fritsch
19. *S. warscewiczii* Perkins

Index to Exsiccatae. Specimens are listed alphabetically by collector. Numbers in parentheses correspond to those in the numerical list of species. If more than one person participated in the collecting, only the first collector listed on the label is cited. Bracketed numbers are taken from the literature and presumed to belong to collections without number or, when following numbers in parentheses (i.e., Matuda and Sharp collections) indicate duplicates of collections where transcription errors apparently occurred.

Abbott, R. Q. 113 (16); 223 (16). Aguilar, J. I. 186 (1); 214 (1); 456 (1); 758 (1); 1335 (19). Aguilar, R. 1126 (6); 1159 (19). Aguirre B., C. 100–51 (15). Alexander, E. J. 1214 (10). Allen, P. H. 4851 (19); 6853 (19); 6882 (19); 7184 (3); 7314 (19). Almeda, F. 2400 (19); 3044 (19); 3291 (19); 3761 (19); 5642 (6). Anderson, W. R. 6109 (15). Andrie 513 (6). Antonio, T. 1640 (19). Aranda, M.

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Valdez, G. L. 616 (2). Valerio, Man. 1378 (1); 1396 (19). Valerio, Mar. 145 (19); 174 (19). Vásquez S., J. 2174 (16). Vázquez, A. 1195 (15); 4164 (15); 4625 (6). Vázquez M., A. 4529 (16). Vela G., L. 2050 (16). Velázquez H., A. 13 (8). Velzen, H. van 2765 (19). Ventura A., F. 784 (6); 866 (6); 1195 (6); 3408 (6); 3511 (6); 5211 (6); 8071 (6); 8116 (6); 12945 (6); 20283 (6); 20303 (6). Vergas, C. 285 (6). Villarreal, L. M. 4585 (8). Villaseñor, J. L. 183 (16). Vincelli, P. C. 424 (19). Voorhies, B. 3–11 (1); 5–3 (1); 16–9 (1).

Walker, S. 72.021 (16); 73H07 (15). Warscewicz, J. 40 (1); 203 (19). Wawra 1011 (6). Weaver, R. E. 1745 (6); 1754 (6). Webster, G. L. 12230 (19); 12496 (11a). Wendt, T. 148b (14e); 582 (14e); 3576 (12?). Werff, H. van der 6301 (19). Wetter, M. A. 2007 (16); 2057 (16). White, G. 70 (19). White, S. S. 5260 (1). Wiemann, M. C. 32 (19). Wilbur, R. L. 1766 (16); 8821 (19); 16166 (19); 16223 (19); 18026 (1); 21135 (19); 22584 (19); 23494 (19); 27228 (19); 29475 (19). Williams, L. O. 10491 (1); 11279 (1); 12136 (1); 12314 (1); 12648 (19); 12709 (1); 13270 (1); 13318 (19); 13581 (19); 13709 (19); 14028 (1); 16067 (1); 16131 (19); 16260 (19); 17455 (19); 20001 (19); 23955 (11a); 24844 (19); 25087 (1); 28194 (19). Woodson, R. E. 484 (19); 919 (19). Woronow, G. 99b (16). Wynd, F. L. 340 (14b).

Yuncker, T. G. 5589 (1); 6175 (6).

Zamora V., N. 1213 (6). Zavala C., F. 295 (6). Zola B., M. G. 526 (6); 612 (6). Zúñiga, R. 169 (6); 575 (6); 607 (1).

Appendix 1. Comparison of Gonsoulin's (1974) treatment of *Styrax* from western Texas, Mexico, and Mesoamerica to the present revision. Synonyms are indented. Specimens of the seven taxa at the end of the right column were not available at the time of Gonsoulin's revision. (D) = deciduous.

Gonsoulin, 1974	Present revision
S. argenteus var. argenteus	S. argenteus
S. panamensis	S. panamensis
	S. radians, *sp. nov.*
	S. austromexicanus, *nom. et stat. nov.*
S. argenteus var. hintonii	S. ramirezii
S. magnus	S. magnus
S. argenteus var. ramirezii	S. ramirezii
S. orizabensis	S. *ramirezii*
S. warscewiczii	S. warscewiczii
	S. steyermarkii, *sp. nov.*
S. conterminus	S. conterminus
S. glabrescens var. glabrescens (D)	S. glabrescens (D)
S. glabrescens var. pilosus (D)	S. glabrescens var. pilosus
S. jaliscanus (D)	S. jaliscanus (D)
	S. gentryi, *sp. nov.*
S. platanifolius var. platanifolius (D)	S. platanifolius subsp. platanifolius (D)
S. platanifolius var. stellatus (D)	S. platanifolius subsp. stellatus, *comb. et stat. nov.* (D)
S. texanus (D)	S. platanifolius subsp. texanus, *comb. et stat. nov.* (D)
S. youngiae (D)	S. platanifolius subsp. youngiae, *comb. et stat. nov.* (D)
	S. platanifolius subsp. mollis, *subsp. nov.* (D)
	S. glabratus
	S. lanceolatus, *nom. et stat. nov.*
	S. incarnatus, *sp. nov.*
	S. nicaraguensis subsp. nicaraguensis, *sp. nov.*
	S. nicaraguensis subsp. ellipsoidalis, *subsp. nov.*
	S. peruvianus
	S. tuxtlensis, *sp. nov.*
Total: 7 species, 11 taxa	Total: 19 species, 24 taxa

Appendix 2. Index to scientific names in taxonomic part. Numbers in parentheses correspond to taxon numbers in the text. Synonyms and excluded names are italicized.

Adnaria Raf. 712
Benzoin Hayne 712
Cyrta Lour. 711
Darlingtonia Torr. 712
Epigenia Vell. 712
  integerrima Vell. (5) 725
Foveolaria Ruiz & Pav. 712
Styrax L. 711
  argenteus C. Presl (1) 714
  var. *grandiflorus* E. Carranza (2) 718
  var. *hintonii* (Bullock) Gonsoulin (16) 747
  var. *micranthus* (Perkins) D'Arcy (16) 747
  var. *parvifolius* E. Carranza (9) 733
  var. *ramirezii* (Greenm.) Gonsoulin (16) 747
  austromexicanus P. W. Fritsch (2) 718
  conterminus Donn. Sm. (3) 720
  cyathocalyx Perkins (16) 747
  diplotrichus Diels 756
  erymophyllus Pohl (5) 725
  gentryi P. W. Fritsch (4) 723
  glabratus Schott (5) 725
  glabrescens Benth. (6) 725
    var. *pilosus* Perkins (6) 727
  guatemalensis Donn. Sm. (6) 727
  hintonii Bullock (16) 747
  incarnatus P. W. Fritsch (7) 730
  jaliscanus S. Watson (8) 731
  lanceolatus P. W. Fritsch (9) 733
  lauraceus Perkins (5) 725
  leiophyllus Miers (5) 725
  limoncillo (Humb. & Bonpl.) Miers 756
  magnus Lundell (10) 734
  micranthus Perkins (16) 747
  myristicifolius Perkins (1) 714
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  orizabensis Perkins (16) 747
  panamensis Standl. (12) 738
  peruvianus Zahlbr. (13) 738
  pilosus (Perkins) Standl. (6) 727
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    subsp. mollis P. W. Fritsch (14b) 742
    subsp. stellatus (Cory) P. W. Fritsch (14c) 743
    subsp. texanus (Cory) P. W. Fritsch (14d) 744
    subsp. youngiae (Cory) P. W. Fritsch (14e) 744
    var. *stellatus* Cory (14c) 743
  polyanthus Perkins (1) 714
  polyneurus Perkins (19) 753
  psilophyllus A. DC. (5) 725
  radians P. W. Fritsch (15) 745
  ramirezii Greenm. (16) 747
    var. *micranthus* (Perkins) Perkins (16) 747
    var. *orizabensis* (Perkins) Perkins (16) 747
  squamulosus M. F. Silva (5) 726
  steyermarkii P. W. Fritsch (17) 751
  texanus Cory (14d) 744
  tuxtlensis P. W. Fritsch (18) 753
  vestitus Lundell (6) 727
  vulcanicola Standl. & Steyerm. (10) 734
  warscewiczii Perkins (19) 753
  youngiae Cory (14e) 744
Strigilia Cav. 711
  argentea (C. Presl) Miers (1) 714
  glabrata (Schott) Miers (5) 725
  leiophylla (Miers) Miers (5) 725
  psilophylla (A. DC.) Miers (5) 725
Tremanthus Pers. 711

SYSTEMATICS OF *KALIMERIS* (ASTERACEAE: ASTEREAE)[1]

Hong-ya Gu[2] *and Peter C. Hoch*[3]

ABSTRACT

The genus *Kalimeris* (Asteraceae: Astereae) comprises a monophyletic group, with the exclusion of section *Cordifolium*, characterized by laterally compressed achenes with short pappus bristles no longer than the length of the corolla tube. This genus of herbaceous perennials is native in East Asia and generally occurs in disturbed habitats. It has close relationships with Asian *Aster* and *Heteropappus*, as revealed by external as well as internal morphological comparisons and cytological studies. Its supposed relationship with the North American genus *Boltonia* is shown to be superficial. The species of *Kalimeris* are all closely related, and comprise a polyploid series ranging from diploid to 12-ploid with $x = 9$. Eight species and ten subspecies of *Kalimeris* are recognized in this treatment.

Kalimeris (Asteraceae: Astereae) is native in East Asia, ranging from the Amur basin in northeastern Asia at 50°N through China, Korea, and Japan to northern Indochina at 16°N, and westward to northern Myanmar (Burma) at 97°E. Most species occur in China. Although it is segregated from *Aster* by most Asian botanists, its taxonomic status as well as its delimitation have been controversial. In order to clarify the taxonomic status of *Kalimeris* and its phylogenetic relationships within Astereae, to establish its infrageneric delimitation and phylogeny, and to improve our understanding of the biosystematically poorly known Asian Astereae, we undertook studies on the morphology, cytology, and geography of *Kalimeris* and some related genera. The results of the cytological study and an RFLP analysis on rDNA of some *Kalimeris* species were published in separate papers (Gu, 1989; Gu & Tara, 1990; Gu et al., 1994). The present treatment was based on results of those surveys, in which we treat *Kalimeris* (excluding sect. *Cordifolium*) as a monophyletic taxon of eight species, distinct from *Aster* and other Asian Astereae.

TAXONOMIC HISTORY OF *KALIMERIS*

The name *Kalimeris* was first published as a subgenus of *Aster* by Cassini in 1822 (see Cassini in King & Dawson, 1975). The only species he described in that subgenus was based on a single cultivated plant that he illegitimately named *Kalimeris platycephala*. In 1825, he elevated the subgenus to generic level based on its distinctive short pappus bristles, conical receptacles, and flat achenes.

Shortly thereafter, Blume (1826) published a monotypic genus, *Asteromoea*, into which he transferred *Aster indicus* L. Subsequent treatments of Astereae by other botanists have differed substantially in the delimitation of *Kalimeris* and *Asteromoea*.

Nees (1832) expanded Cassini's concept of *Kalimeris* by transferring into it four species of *Aster* with longer pappus bristles; these were treated in the genus *Heteropappus* in most subsequent treatments by other botanists. Nees maintained *Asteromoea* as a distinct monotypic genus. He altered *Kalimeris* to *Calimeris*, a spelling that has been

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